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PALAEONTOLOGY

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ACTOSTROMA GEN. NOV., A JURASSIC STROMATOPOROID FROM MAKTESH HATHIRA, ISRAEL

by R. G. S. HUDSON

ABSTRACT. Stromatoporoids from the Coral-stromatoporoid beds (Upper Jurassic: Argovian–Rauracian) exposed in the Kurnub Anticline of Maktesh Hathira, southern Israel, are shown to be characterized by lateral astrotubes and considered to be transitional to the Hydroidea. They are described as *Actostroma damesini*, *A. nasri*, and *A. kühni*, gen. et spp. nov.

INTRODUCTION

THE Jurassic succession (Callovian to Tithonian) exposed in the Kurnub Anticline at Wadi Hathira, about 35 kilometres south-east of Beersheba, northern Negev, southern Israel, includes, near the top of the succession, 58 metres of limestone and marl with abundant corals and stromatoporoids. The fauna is of Rauracian facies and of Upper Argovian (Rauracian) age. The stromatoporoids include various species of *Promillepora*, *Shuqraia*, *Steinerina*, and *Stromatoporina*, *Shuqraia* being by far the most common. *Promillepora kurnubi* Hudson, *P. pervinquieri* Dehorne, *P. douvillei* (Dehorne) and *Steinerina somaliensis* (Zuff.-Com.) were described from these beds (Hudson 1956). A generalized account of the Jurassic succession is given by Blake (1936), Shaw (1947), Ball and Ball (1953), and Wiener (1955). The specimens described in this paper were collected by the author. Registration numbers preceded by the Letter H are those of specimens in the collection of the Department of Palaeontology, British Museum (Natural History), London.

The author here records his thanks to those geologists of the Iraq Petroleum Company whose work made this paper possible and in particular to F. E. Wellings, Chief Geologist, who first investigated the area and to L. Damesin who, with S. Nasr, mapped the area and introduced the author to it. Permission to publish this paper has been generously given by the Directors and Chief Geologist of the Iraq Petroleum Company.

STROMATOPOROID SKELETAL MORPHOLOGY

Methods of investigation. The internal structure of the stromatoporoids described in this paper was first investigated by the examination of tangential and radial thin-sections. Examination by transmitted light of the tangential sections failed to distinguish between shallow structures such as coenosteal tubules and those, such as the astrotubes, that have depth, a defect only partly remedied by the examination of the thin sections by reflected light (Pl. 16, figs. 4–6). The two types of structures are, however, very distinct on polished surfaces where the deeper structures are darker in colour (Pl. 16, figs. 8–14). Internal structure was, therefore, mainly investigated by the examination of serial polished surfaces.

The measurements of pillars, lamellae, coenosteal tubules, &c., recorded in the follow-

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ing descriptions of the various species are very approximate. They indicate the commonly occurring dimensions and not the average, or the range.

Lamellae. The skeletal elements of the Palaeozoic Stromatoporoidea consist, in the main, of vertical pillars or vertical lamellae, and transverse laminae. In many genera these are histologically different and thus there is justification for the distinction inferred by the use of the terms lamellae and laminae. In the Mesozoic Stromatoporoidea vertical and horizontal elements have a similar structure and origin, and are therefore both denoted lamellae and distinguished as vertical lamellae and transverse lamellae.

Latilamellae. These are the concentric zones of the reticulum, alternately the one lighter in colour than the other (Pl. 16, figs. 7–14), a colour difference occurring in both the skeletal elements and the spaces between them. The difference is partly due to an actual difference in the colour of the skeletal elements, due to a variation in texture of the skeletal tissue, and partly due to the greater thickness of pillars and transverse lamellae in the lighter coloured (compact-textured) zone. This reduces the size of the spaces between the skeletal elements and so, having less depth, they are, by reflected light, lighter in colour. There are also occasional thinner bands in which the transverse lamellae are more or less as equally developed as the vertical lamellae, thus giving a marked reticulation in radial section (Pl. 16, figs. 11, 14). They may include transverse lamellae of considerable continuity.

Skeletal tissue. The tissue of the pillars and lamellae of the Mesozoic stromatoporoids is essentially trabecular formed by radial or bilateral secretion, normally crystalline and fibrous, continuing from retreating areas of calcification and forming, in the case of a pillar, calcite fibres radial to an axial strand of superposed 'centres of calcification' or trabecular centres. In the case of a lamella such strands laterally coalesce to form a median band of trabecular centres. Such trabecular strands or median bands are finely granular and are usually darker than their sheath of fibres. They may be simple, that is, formed of superposed single centres, or composite, formed of superposed groups of centres. Such groups may be loose or compact, and may form the entire trabecula. The angular relationship of the fibres to the axial strand or median band varies. They may be, as in *Actinostromaria*, perpendicular, radially in the pillar, bilaterally in the lamellae. Such skeletal tissue is here termed *orthogonal.* They may diverge upwards, again radially or bilaterally, as in *Stromatoporina*, a form of divergence often termed as 'fasciculate upwards' or 'fountain-like (*jet d'eau*)'. Such skeletal tissue is here termed *clinogonal.* When the trabecular strands or bands are composite, the angle of divergence of the fibres varies, though more generally outwards than upwards. The fibres may be generally perpendicular to the axis or diverge slightly upwards, though rarely clearly defined or constant: when the centres are isolated the fibres may approximate to sphaerical radial. Such tissue is here termed *heterogonal.*

It is doubtful if the tissue of *Burgundia* could be called trabecular. It is due to unilateral secretion of fibres perpendicular to a plane of calcification centres. Such tissue is termed *unilateral orthogonal.*

Astrorhizae and astrorhizal systems. In its simplest form, the stromatoporoid astrorhizal system consists of a number of shallow, radiating furrows or gutters on the surface of the coenosteum, without walls, branching distally, and passing distally without a marked break into the reticulum; they may join at the centre or there may be, at the centre, one or more shallow depression or pits. It is these furrows which were originally called astrorhizae and it is with that meaning the term is used in this paper. The astrorhizae may, or may not, be incorporated into the coenosteum by subsequent growth of the reticulum. When they are they form astrorhizal lateral tubes, horizontal or oblique, according as to whether the surface on which they formed was level or axially raised.

Astrotubes. In many Mesozoic stromatoporoids the axial part of the astrorhizal system consists of one or more closely grouped vertical tubes, wider than the coenosteal tubules and usually tabulate. These vertical tubes are here called axial astrotubes. In *Stromatoporellina*, *Milleporella*, and such forms as '*Stromatopora*' *choffati* Dehorne, the wide tabulate astrorhizae are divided into chambers of varying length, some, especially near the axis, being almost circular. They continue in depth so that in vertical section they are variously exposed as tabulate vertical tubes: cut obliquely, as they often are in vertical sections, they appear as tabulate lateral chambers. In *Steinerella* the process of isolation of these chambers is carried still farther and, distally, the astrorhizal radii may include of a number of tabulate vertical tubes, adjacent or separate, though clearly aligned. In the species of *Actostroma* described in this paper, there are, variously distributed within the coenosteum, a number of such vertical tubes. They are, more or less, linearly arranged about an axis, the lines of tubes branching distally in a pattern comparable to that of the astrorhizae of the more simple systems. It is suggested that all such vertical tubes, whether occurring along astrorhizae or aligned in a comparable pattern, should be termed lateral astrotubes.

Lateral astrotubes originate from coenosteal tubules in astrorhizae or along the astrorhizal radii. Their abundance, the pattern they form, and their direction of upward growth varies with the species. They are independent of the latilamellae. When, as in *Actostroma*, they do not occur in astrorhizae, their relationship to the astrorhizal system is shown not only by their alignment but sometimes by the specialization, to a variable degree, of the coenosteal tubules separating them along the radii. In *Actostroma nasri*, for instance, such tubules are elongated in the direction of the radii and are thus aligned. They are also generally slightly larger than those in the main reticulum. This difference continues in depth so that in vertical sections, the astrorhizal radii, apart from the lateral astrotubes, are marked by coenosteal tubules which are continuous, slightly wider and more regularly reticulate than the remainder (Pl. 16, fig. 14). When such a link does not exist and the astrotubes are only vaguely aligned, as in *Actostroma damesini*, they approach the autotubes of the Milleporidiidae which have no alignment. The two structures are analogous.

Astrorhizal symmetry. In *Actostroma nasri* and *A. kühni* there are six main astrorhizal radii (see Pl. 16, figs. 7, 9, 13), usually in two groups of three. This sixfold symmetry also occurs in *Actostromaria stellata* Haug (see Steiner 1932, p. 38). Though the pattern is confused by early bifurcation, the figures (Steiner 1932, pl. 3) of *Actinostromaria lugeoni* Steiner also suggest sixfold astrorhizal symmetry. These and other examples suggest that a sixfold astrorhizal symmetry is characteristic of the Actinostromariidae. In other stromatoporoids the pattern of the astrorhizal radii is also sixfold and it may be that the basic astrorhizal symmetry of other groups is also hexameral.

SYSTEMATIC PALAEONTOLOGY

Classification. The Jurassic–Cretaceous hydrozoa which have been compared to the Palaeozoic Stromatoporoidea can be divided into two groups, those such as the Milleporidiidae, without astrorhizae or related structures, and those such as the Stromatoporinidae, Actinostromariidae, and Burgundiidae which have astrorhizae or related structures. The former group have been considered to belong to the Hydroidea (comprising, with others, all recent hydrozoa with a calcareous skeleton, including the Milleporina and the Stylasterina) and the latter to the Stromatoporoidea (Kühn 1928, 1939; Alloiteau 1952; Hudson 1956). Galloway and St. Jean (1956) and St. Jean (1957), however, consider that, on the basis of tissue structure, only Palaeozoic forms should be included in the Stromatoporoidea and that the Mesozoic forms should be allocated to the Sphaeractinoidea.

The author, however, considers that the occurrence in both Palaeozoic and Mesozoic forms of astrorhizal structures is the most important diagnostic feature of both groups, possibly the only one of phylogenetic significance and, as such, it justifies the inclusion in the Stromatoporoidea of those Mesozoic forms in which it occurs. Nevertheless, the difference in the microstructure of the skeletal tissue of Palaeozoic and Jurassic–Cretaceous forms is, in the opinion of the author, a fundamental one and, by and large, excludes the Jurassic–Cretaceous stromatoporoids from the families into which the Palaeozoic forms are grouped. The thesis that various groups in the Stromatoporoidea are ancestral to various groups in the Hydroidea is possibly a true one: it cannot, however, be demonstrated and should not, as yet, be taken into account in classification.

The various families of the Jurassic–Cretaceous Stromatoporoidea can be grouped according to the direction of growth of the fibres of the skeletal tissue and the grouping of the trabecular centres. There are those families, such as the Stromatoporinidae and Milleporellidae, in which the fibres are bilaterally clinogonal, those, such as the Actinostromariidae, in which they are bilaterally orthogonal or heterogonal, and those, such as the Burgundiidae, in which they are unilaterally orthogonal. It is not considered advisable to give these groups taxonomic rank until further work has been done on the structure of the skeletal tissue.

Order STROMATOPOROIDEA

Family ACTINOSTROMARIIDAE Hudson 1955

Diagnosis. Stromatoporoidea with orthogonal reticulum of vertical and transverse lamellae. Skeletal tissue orthogonal or heterogonal. Astrorhizal system of axial astrotubes and astrorhizae, or, of lateral astrotubes with, or without, astrorhizae.

Remarks. The above diagnosis is framed to include two groups of genera: one including the nominate genus *Actinostromaria* Haug 1909 (type species *A. stellata* Haug 1909) and the allied genus *Actinostromarianina* Lecompte 1952 (type species *A. dehorneae* Lecompte 1952); the other including the genera *Stromatorhiza* Bakalow 1906 and *Actostroma* gen. nov. All the above have an orthogonal reticulum but differ in the structure of their skeletal tissue, which in the first group is bilaterally orthogonal, and in the second group is bilaterally heterogonal. The enlargement of the family diagnosis to include such different genera is justified by the great similarity of their reticulum and by the consideration that, in the opinion of the author, such heterogonal tissue is ancestral to orthogonal tissue. The above genera are divorced from the Actinostromatidae Nicholson 1886, in which some of them have been included, because of the difference of their fibrous skeletal tissue from the compact skeletal tissue of *Actinostroma* (Lecompte 1956, p. F127).

In a recent paper (Hudson 1957) *Stromatorhiza granulosa* (Koby) was redescribed, its characteristic structures shown to be an orthogonal reticulum, heterogonal skeletal tissue, astrorhizae, and astrotubes. The genus was placed in a new family, the Stromatorhizidae, characterized by heterogenal tissue and thus distinct from the Actinostromariidae then defined by definite orthogonal tissue only. The family Actinostromariidae as now redefined would include *Stromatorhiza*: the family Stromatorhizidae is therefore no longer required.

Genus ACTOSTROMA gen. nov.

Type species *Actostroma damesini* sp. nov.

Diagnosis. Actinostromariidae with nodular encrusting coenosteum and orthogonal latilamellate reticulum of dominant vertical pillars linked by discontinuous transverse bars or lamellae. Coenosteal surface even, with open-vermiculate or tubular ostea. Skeletal tissue heterogonal, of feebly developed fibres, irregularly perpendicular or slightly diverging upwards from a broad composite axial strand or median band of trabecular centres. Lateral astrotubes abundant. Astrorhizae present or absent. No lateral astrorhizal tubes. Tabulae virtually absent or present only in astrotubes.

Remarks. The distribution of the astrotubes and the complete lack of astrorhizae in *Actostroma damesini* is unique and justifies the founding of a new genus. But for the feeble radial alignment of the astrotubes which indicate an astrorhizal origin, the species could quite well have been considered as an hydroid and not a stromatoporoid. The widening of the genus to include *A. kühni* characterized by astrorhizae is perhaps not justifiable. The certain allocation of that species awaits the clarification of Germovšek's genera discussed below.

The hydrozoan fauna described by Germovšek (1954) from the Upper Jurassic (Tithonian) of Slovenia, Yugoslavia, includes stromatoporoids characterized by a nodular coenosteum, an orthogonal reticulum, and vertical tubes. These were all considered to be new species and, generically, variously allocated to *Actinostroma* Nicholson, *Actinostromaria* Haug, and the three new genera, *Actinostromina* Germovšek, *Astrostylopsis* Germovšek, and *Trupetostromaria* Germovšek.

Some of Germovšek's species have considerable resemblance to the species of *Actostroma* described in this paper and the question arises as to whether *Actostroma* is a synonym of one or other of Germovšek's genera. Unfortunately the illustrations of his species do not include those of tangential surfaces or thin-sections in which a pattern of astrotubes, the main diagnostic feature of *Actostroma*, could be seen nor are his descriptions adequate since there is lack of definition of the various structures to which he refers: 'astrorhizal branches', for instance, might be astrorhizae or lateral astrotubes. The only illustration, for instance, of *Actinostromaria tubulata* Germovšek is that of a radial section which might be that of a species of *Actostroma*.

The forms most like species of *Actostroma* are those allocated to his new genera *Astrostylopsis* and *Trupetostromaria*, both of which are erroneously allocated to a family Trupetostromidae Germovšek 1954 on a mistaken structural similarity to its designate genus *Trupetostroma* Parks 1936, a genus of Devonian age. Both *Astrostylopsis* and *Trupetostromaria* are, like *Actostroma*, characterized by a skeletal tissue which is more or less heterogonal and both, again like *Actostroma*, have abundant vertical tubes. Those in *Astrostylopsis* are sporadically distributed in the coenosteum (Germovšek 1954, pl. 7, fig. 1*b*) and are considered by Germovšek to be individual axial tubes. In *Trupetostromaria* they are extensively and fairly closely distributed in the coenosteum and are also considered by Germovšek to be individual axial tubes. In neither genera is there evidence of alignment of astrotubes, the diagnostic feature of *Actostroma* gen. nov. The equation of *Astrostylopsis* with *Stromatorhiza* Bakalow (Hudson 1957) is now considered premature.

In 1955 Yabe and Sugiyama founded a genus *Tosastroma* which they placed in the Milleporellidae and to which they allocated two species, *T. tokunagai* Y. and S. (by original designation the type species) and *T. kiiensis* Y. and S. The types of both species are from the Torinosu Limestone (Upper Jurassic) of Japan. The author is of the opinion that the two species are not cogeneric. *T. kiiensis* has an orthogonal reticulum of irregular vertical pillars and transverse bars, the former dominant, the latter very discontinuous, a pattern very much like that of *Actostroma damesini*. Within the reticulum there are bands in which the vertical pillars are coarser and closer, again very much like *A. damesini*, but differing from that species in that the transverse elements in these bands are tabulae. Scattered in the reticulum but not mentioned by Yabe and Sugiyama, are wider unwalled tubes which might quite well be astrotubes, though they have no alignment. No indication is given of the tissue structure. In the opinion of the author *T. kiiensis* should be placed in the Actinostromariidae. Its bands of tabulate reticulum exclude it from *Actostroma*. It is evidently a closely allied form possibly demanding a new genus.

It is possible that *Actinostroma presalevensis* Zuff.-Com. and *Actinostromaria darroensis* Zuff.-Com. from the 'Oolitico medio' (Lusitanian) of Italian Somaliland and Ethiopia (Zuffardi-Comerci 1932; Wells 1943) are species of *Actostroma*. It has not, however, been possible to locate the type specimens of these species and since the description and figures are inadequate, generic determination has not been possible.

Actostroma damesini sp. nov.

Plate 15, figs. 1, 4; Plate 16, figs. 3, 5, 8, 10; Plate 17, figs. 3–5, 9; text-figs. 1–3

Type specimens. Holotype: H 4890, two pieces and thin-sections *a*, *b* (Pl. 15, fig. 1; Pl. 16, figs. 3, 5, 8, 10; Pl. 17, fig. 9; text-fig. 3). Paratypes: H 4888, one piece and thin-sections

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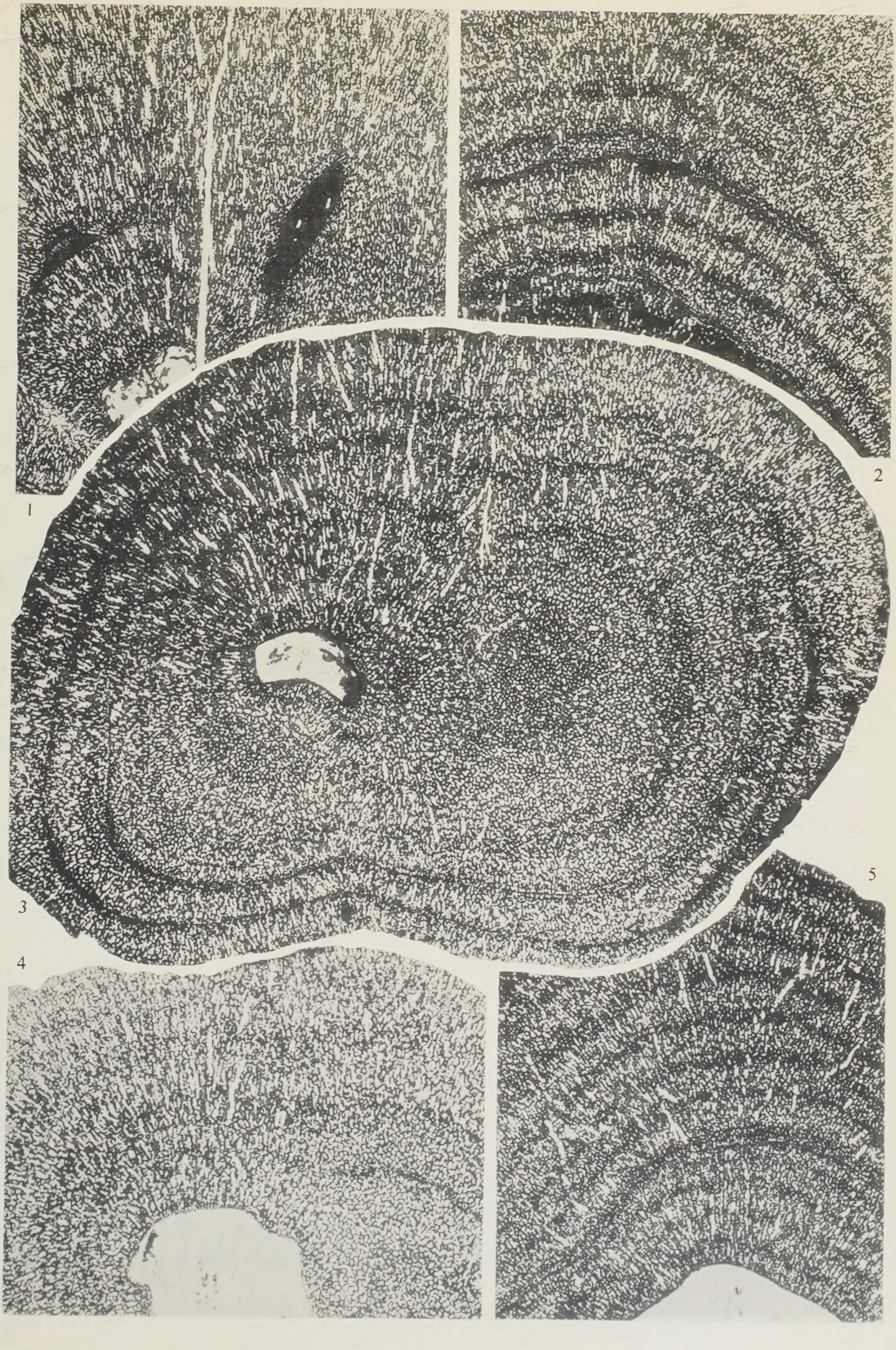
EXPLANATION OF PLATE 15

Thin-sections, photographed by transmitted light and untouched, of specimens from Coral-stromatoporoid beds, Kurnub Limestone (Upper Jurassic), Maktesh Hathira, Israel. The darker bands are the compact latilamellae (light-coloured in reflected light) in which the skeletal elements tend to be lamellae rather than pillars. On this plate the fine mesh of these bands is not always shown so that the band appears more compact and darker than it actually is.

Figs. 1 and 4. *Actostroma damesini* sp. nov. 1, radial section, H 4890a, ×4·1, from holotype, showing unwalled lateral astrotubes. 4, oblique and, lower right, tangential section, H 4889b, ×5·2, showing initial reticulum.

Figs. 2, 3, and 5. *Actostroma nasri* sp. nov. 2, radial section, H 4891b, ×4·1, showing latilamellae of alternate bands of open and compact reticulum. 3, upper right, radial section, remainder oblique or tangential, H 4892a, ×4·1, showing axial and lateral astrotubes in transverse and longitudinal sections. 5, radial section, H 4893b, ×4·1, from holotype, showing latilamellae.



HUDSON, *Actostroma* gen. nov.

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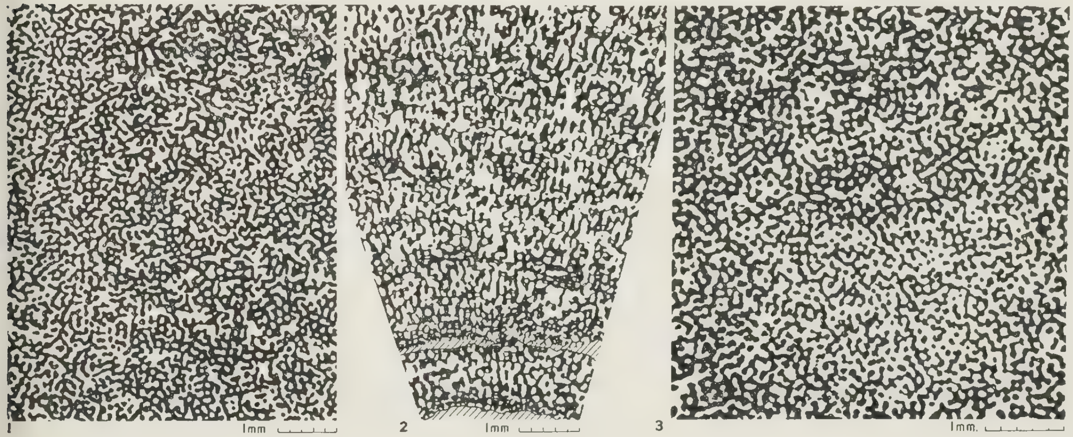
a, *b* (text-figs. 1, 2); H 4889, one piece and thin-sections *a*, *b*, *c* (Pl. 15, fig. 4; Pl. 17, figs. 3–5). From the Coral-stromatoporoid beds (Argovian), Kurnub Limestone, Maktesh Hathira, Israel.

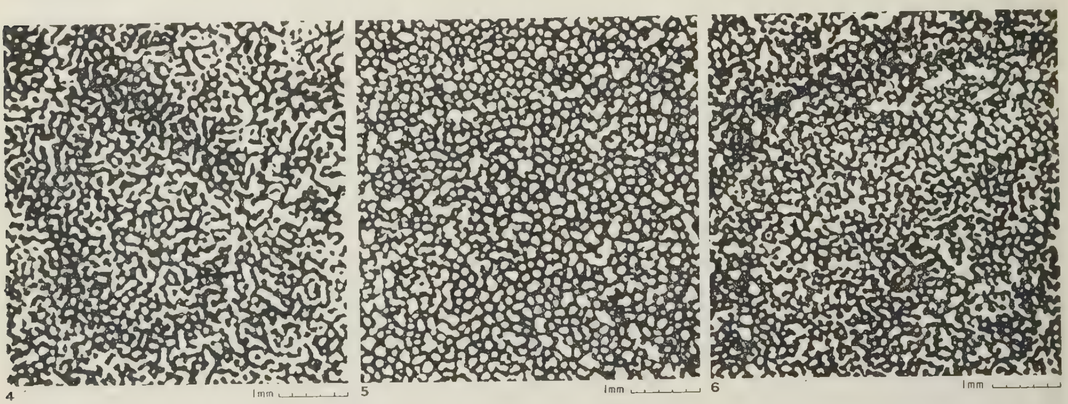
Diagnosis. *Actostroma* with slightly latilamellate coenosteum. Reticulum of irregular pillars, mainly continuous, and short transverse bars; transversely vermiculate or tubular, tubules *c*. 0·05–0·07 mm. across, pillars *c*. 0·05–0·07 mm. thick. Transverse bars *c*. 0·05–0·07 mm. thick, and *c*. 0·07 mm. apart. Astrotubes, *c*. 0·1 mm. across, open to adjacent coenosteal tubules, and hence transversely irregularly stellate, abundant, evenly and well spaced; astrorhizal alignment slight. No astrorhizae.



TEXT-FIGS. 1–3. *Actostroma damesini* sp. nov., drawn from photographs of thin-sections. In all three sections the alternating latilamellae are shown by areas of compact and open reticulum. Fig. 1, Tangential section of H 4888b, showing open astrotubes. Fig. 2, Oblique section of H 4888a, showing astrotubes and fine orthogonal reticulum of initial growth, renewed after lime-mud sedimentation (represented by oblique lines). Fig. 3, Tangential section of H 4890b, holotype, showing pillars and pillar-lamellae, astrotubes, and compact and open reticulum.

Description. Coenosteum nodular (largest 4 by 4 by 3 cm.), encrusting, enveloping, mainly corals and stromatoporoids. Surface of fine irregular ostea, with scattered unwalled ostea of astrotubes. No mamelons, no astrorhizae. Coenosteum faintly latilamellate with alternate bands of compact-textured (light-coloured) and open-textured (dark-coloured) reticulum: colour difference due, in part, to difference in proportion of trabecular centres in tissue.

Reticulum of fairly continuous irregular pillars (about 17 in 2 mm.) with, perpendicular to them, discontinuous, very short, transverse connecting processes similar to pillars, forming, in tangential section, a generally tubular mesh in the compact reticulum, and a vermiculate mesh, with many isolated pillars, in the open reticulum. Difference between latilamellae not marked, partly due to thicker pillars and slightly longer transverse bars in compact reticulum. Initial layer of reticulum, about 0·7 mm. thick, finely orthogonal with tubules about half normal width (Pl. 17, figs. 3, 4) and transverse lamellae more continuous. Skeletal tissue almost entirely of trabecular centres, dark, finely mottled and granular, with scattered darker nuclei; outer zone of lighter granular tissue in which grains tend to be elongated or fibrous and generally radially perpendicular (hetergonal). Dark zone of trabecular centres in transverse structures tends to be narrower, less diffuse, and better defined. Tabulae, in astrotubes, transitional in character to transverse structures.



TEXT-FIGS. 4–6. *Actostroma nasri* sp. nov., drawn from photographs of tangential thin-sections. Fig. 4, H 4893a, from holotype, showing traces of astrorhizae within coenosteum, and areas of compact and open reticulum (latilamellae). Fig. 5, H 4892b, compact reticulum showing lateral astrotubes and entire coenosteal tubules. Fig. 6, H 4891a, slightly oblique, showing areas of compact and open reticulum.

Astrotubes, abundant, radial, fairly straight and parallel, unwalled, *c.* 0·1 mm. across, communicating laterally with adjacent coenosteal tubules and thus roughly cruciform, appearing wider in radial section, and difficult to distinguish in tangential section (text-

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EXPLANATION OF PLATE 16

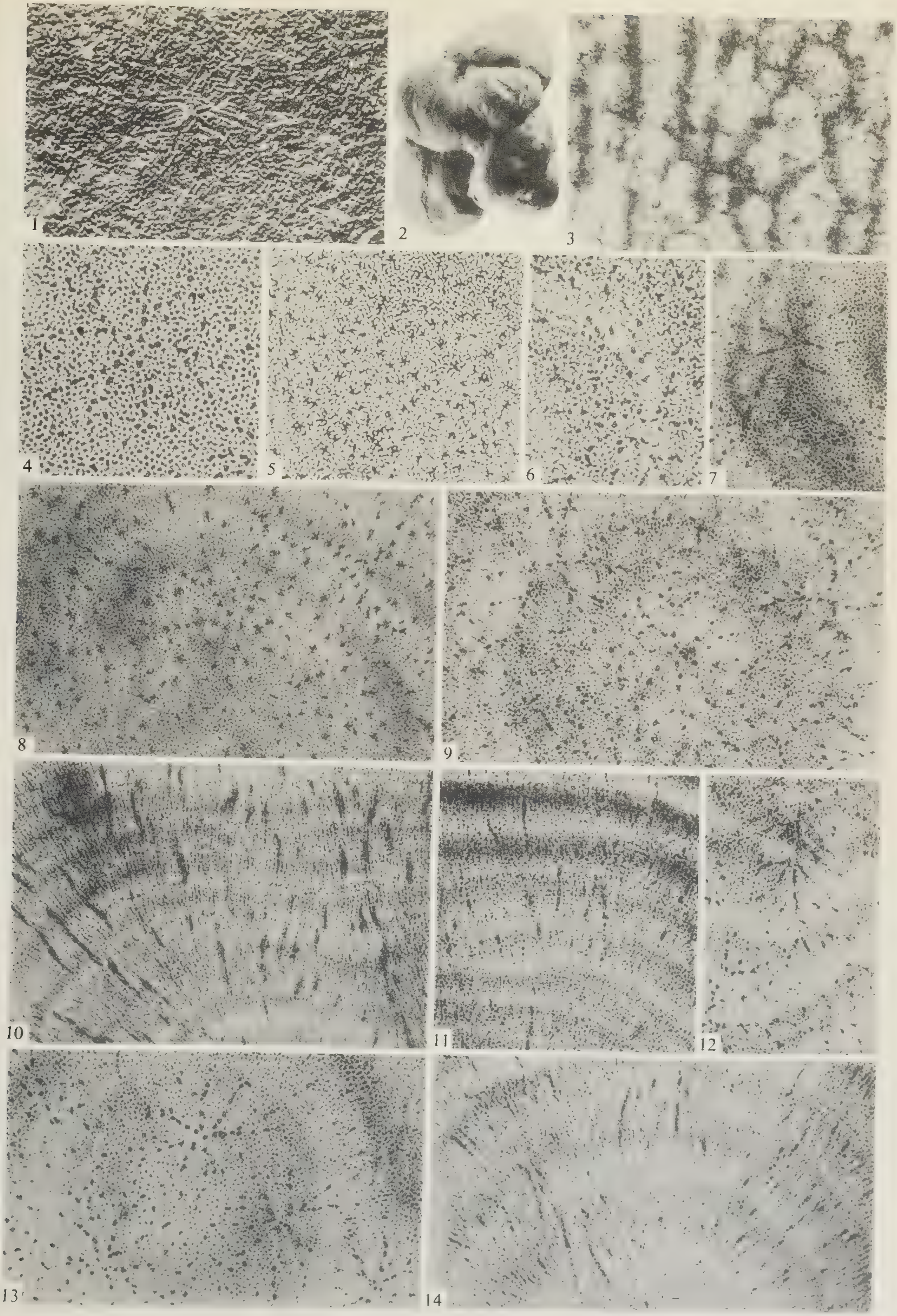
All specimens from Coral-stromatoporoid beds, Kurnub Limestone (Upper Jurassic), Maktesh Hathira, Israel. Thin-sections (figs. 4–6) and polished surfaces (figs. 7–14), photographed by reflected light and untouched.

Figs. 1, 2, 9. *Actostroma kühni* sp. nov., all of holotype. 1, coenosteal surface, H 4887, ×7, showing astrorhizae connecting ostea of lateral astrotubes. 2, nodular coenosteum, H 4807, ×0·5. 9, tangential surface, H 4887, ×5, showing astrorhizal arrangement of astrotubes.

Figs. 4, 6, 7, 11–14. *Actostroma nasri* sp. nov. 4, tangential section, H 4892b, ×6·5, showing astrorhizal arrangement of astrotubes. 6, tangential section, H 4891a, ×6·5, showing astrotubes and compact and open latilamellae. 7, tangential surface of H 4893/1, ×5, from holotype, showing latilamellae and lateral astrotubes linked by specialized coenosteal tubules. 11, radial surface of H 4893/1, ×5, from holotype, showing latilamellae and astrotubes. 12, oblique surface of H 4891/2, ×5, showing two adjacent systems of astrotubes and connecting coenosteal tubules. 13, tangential surface of H 4892, ×5, showing isolation of astrotubes outside astrorhizal grouping. 14, radial surface of H 4892/1, ×5, showing astrotubes, and coenosteal tubules of astrorhizal radii.

Figs. 3, 5, 8, 10. *Actostroma damesini* sp. nov., all of holotype. 3, thin-section, H 4890a. Photographed, ×52, by transmitted light. Showing heterogonal tissue of vertical and transverse lamellae. 5, tangential section, H 4890b, ×5·75, showing astrotubes joining with adjacent coenosteal tubules. 8, tangential surface, H 4890/1, ×5, showing in centre astrorhizal arrangement of astrotubes. 9, radial surface, H 4890/1, ×5, showing latilamellae and widening of astrotubes due to joining with adjacent coenosteal tubules.

PLATE 16



HUDSON, *Actostroma* gen. nov.

fig. 3). Originate from specialized coenosteal tubules, slightly straighter and with more regular transverse lamellae than normal. More or less radially aligned in widely branching astrorhizal pattern, alignment and pattern indefinite distally; some apparently independent of astrorhizal pattern. Astrorhizal systems close and distally interwoven so that astrotubes fairly evenly distributed, *c.* 0·3 to 1·0 mm. apart. No definite axial astrotubes. Astrotubes not elongated along astrorhizal radii; coenosteal tubes between astrotubes on radii not specialized. No lateral astrorhizal tubes.

Actostroma nasri sp. nov.

Plate 15, figs. 2, 3, 5; Plate 16, figs. 4, 6, 7, 11–14; Plate 17, figs. 1, 10; text-figs. 4, 6

Type-specimens. Holotype: H 4893, two pieces and thin-sections *a*, *b* (Pl. 15, fig. 5; Pl. 16, figs. 7, 11; Pl. 17, figs. 1, 10; text-fig. 4). Paratypes: H 4891, two pieces and thin-sections *a*, *b* (Pl. 15, fig. 2; Pl. 16, figs. 6, 12; text-fig. 6). H 4892, two pieces and thin-sections *a*, *b* (Pl. 15, fig. 3; Pl. 16, figs. 4, 13, 14; text-fig. 5). From the Coral-stromatoporoid beds (Argovian), Kurnub Limestone, Maktesh Hathira, Israel.

Diagnosis. Actostroma with very latilamellate coenosteum. Reticulum continuously tubular, occasionally vermiculate, tubules *c.* 0·05–0·1 mm. across, pillars *c.* 0·05 mm. across. Transverse lamellae well developed; *c.* 0·05 mm. thick and *c.* 0·07–0·1 mm. apart. Lateral astrotubes abundant, *c.* 0·1–0·15 mm. across, walled by coenosteal tubules, often elongate and closely spaced, and with branching alignment of astrorhizal pattern. Loosely grouped axial astrotubes. Coenostral tubules between astrotubes may be aligned and more regular than normal.

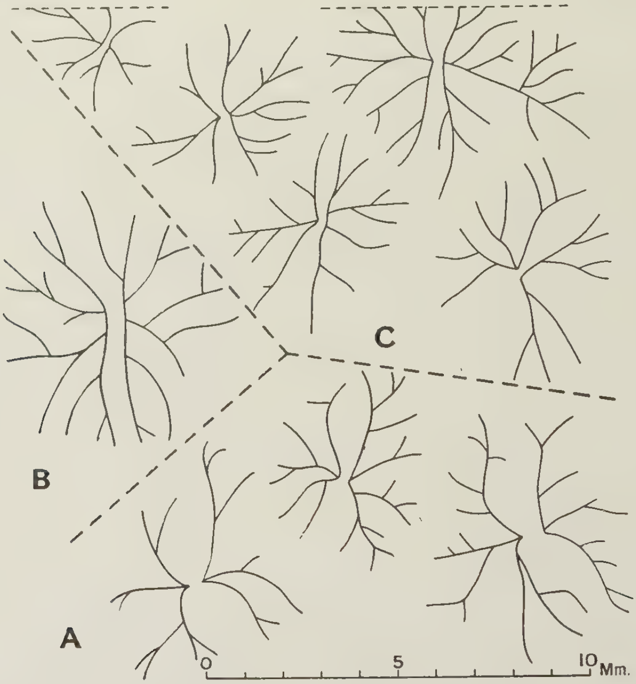
Description. Reticulum, of vertical pillars, continuous, dominant, 15 in 2 mm., and transverse structures equally common, but rarely continuous across a pillar; mainly tubular or polygonal in tangential section and orthogonal in radial section. Compact (*c.* 1–1·5 mm. thick) and open-textured (*c.* 1·5–2 mm. thick) latilamellae, difference partly due to thickness of pillars. Occasional narrow bands in which transverse structures may be continuous. Fine orthogonal initial reticulum. Tissue of composite trabecular centres, with outer zone elongate granular or indifferently fibrous and indefinitely heterogonal. Trabecular strand wide in pillars of lighter-coloured latilamellae, narrow in dark-coloured, hence difference in colour.

Most astrotubes radially aligned, the radii branching at a wide angle with astrorhizal pattern; distally they are scattered and independent of radii. Astrotubes elongated, walled, evenly spaced along the radii, usually separated by two coenosteal tubules, aligned and elongated, an arrangement which continues in depth. These specialized coenosteal tubules show well in tangential and radial sections, are more regular than the normal tubules but not as dark in colour as the astrotubes. All the lateral astrotubes originate in such specialized coenosteal tubules. The diameter of the astrotubes is such that on the surface of the coenosteum their ostea are rarely distinct from those of the coenosteal tubules. Nevertheless, careful rubbing down of tangential surfaces has shown that the astrorhizal system of astrotubes and coenosteal tubules exists in places within the coenosteum as irregular radial and extremely shallow chambers (text-figs. 5 and 6), so shallow that they are not discernible on radial surfaces. Tabulae are not uncommon in the astrotubes.

Actostroma kühni sp. nov.

Plate 16, figs. 1, 2, 9; Plate 17, figs. 2, 6–8, 11

Type specimen. Holotype: H 4887, two pieces and thin-section *a* (Pl. 16, figs. 1, 2, 9; Pl. 17, figs. 2, 6–8, 11). From the Coral-stromatoporoid beds (Argovian), Kurnub Limestone, Maktesh Hathira, Israel.



TEXT-FIG. 7. Astrorhizal pattern of A, *Actostroma kühni*, H 4887; B, *A. damesini*, H 4890/1; C, *A. nasri*, H 4892/2.

Diagnosis. Actostroma with latilamellate coenosteum. Surface with astrorhizae (5–6 mm. across). Reticulum irregularly orthogonal but equally developed, mainly tubular, tubules

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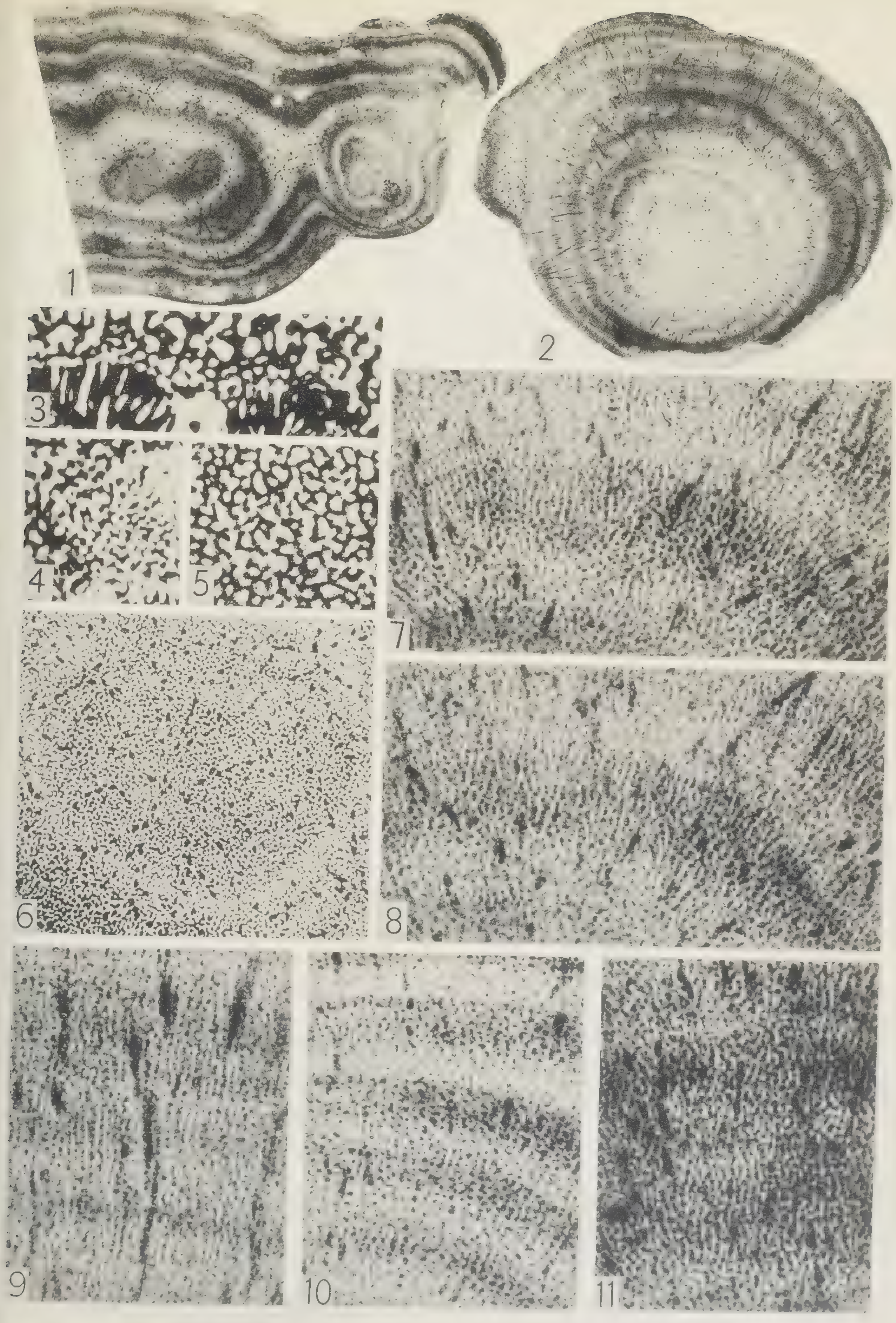
EXPLANATION OF PLATE 17

All specimens from Coral-stromatoporoid beds, Kurnub Limestone (Upper Jurassic), Maktesh Hathira, Israel. Thin-sections photographed by transmitted light (figs. 3–5), by reflected light (fig. 6), and polished surfaces (figs. 1, 2, 7–11). All untouched.

Figs. 1, 10. *Actostroma nasri* sp. nov., both of holotype. 1, tangential surface of H 4893/1, ×2, showing latilamellae. 10, radial surface of H 4893/2, ×10, showing reticulum pattern.

Figs. 3–5, 9. *Actostroma damesini* sp. nov. 3, 4, H 4889b, ×30, showing initial reticulum. 3, radial section of *Actostroma* on bryozoa. 4, tangential section of fine initial reticulum. 5, tangential section, H 4889a, ×15, showing pillars and connecting transverse bars. 9, radial surface of holotype, H 4890/2, ×2, showing reticulum pattern.

Figs. 2, 6–8, 11. *Actostroma kühni* sp. nov., all of holotype. 2, tangential and radial surface of H 4837/1, ×2, showing latilamellae. 6, tangential section, H 4887a, ×60, showing astrorhizal pattern of astrotubes. 7, 8, oblique surfaces, 1 mm. apart, of H 4887/2, ×10, showing individuality of astrotubes. 11, radial surface of H 4887/1, ×10, showing reticulum pattern.



HUDSON, *Actostroma* gen. nov.

c. 0·7–0·1 mm. across, walls and transverse bars *c.* 0·05–0·08 mm. thick. Lateral astrotubes abundant, *c.* 0·1–0·15 across, closely spaced, often adjacent and elongated, aligned with branching astrorhizal pattern. Axial astrotubes. Specialized coenosteal tubules abundant.

Description. Nodular (reniform) coenosteum (Pl. 16, fig. 2) with surface of ostea and shallow astrorhizae (Pl. 16, fig. 1). No mamelons. Reticulum latilamellate with compact and open-textured bands. Dominant, irregular, fairly continuous, vertical pillars (15 in 2 mm.) and abundant transverse bars linking the pillars but rarely continuous across more than one tubule (Pl. 17, fig. 11). Transverse reticulum pattern a fine net of small irregular tubules, mostly indefinitely polygonal; radial pattern, an irregular reticulate mesh in which transverse bars are well developed. Tabulae occur in astrotubes and coenosteal tubules of astrorhizal radii. Tissue indefinitely heterogonal with wide composite band of trabecular centres.

Lateral astrotubes with much-branched astrorhizal alignment. Main branches of astrorhizal system in two groups of three. Specialized coenosteal tubules seen in radial section as straight and with evenly spaced transverse bars, but hardly evident in tangential section.

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ON *CEPHALASPIS LYELLI* AGASSIZ

by ERROL WHITE

Abstract. The type specimen of *Cephalaspis lyelli*, the genotype of *Cephalaspis*, has never been fully described nor properly figured, and its counterpart has hitherto been completely ignored. Both parts of the specimen have been further developed, especially the counterpart, and are here described in detail. The position of the species in Stensiö's proposed new classification is established on the form of the oralo-branchial chamber. No other specimen of this species is known.

INTRODUCTION

It is a remarkable fact that *Cephalaspis lyelli* Agassiz, the type-species of *Cephalaspis* and therefore the basis of the whole group of the Osteotraci or Cephalaspidomorphi, has never been properly defined nor the unique type-specimen adequately described. Until now this has not been of much consequence since cephalaspids are of characteristic form and easily recognized, while the genera comprising the group have been readily distinguishable on external characters. My friend Professor Stensiö has allowed me the privilege of reading parts of the proofs of his article for the *Traité de Paléontologie*, and in it he is proposing a classification in which the numerous species now referred to the genus *Cephalaspis* are divided among three genera in as many different Orders or Suborders. The basis of this remarkable proposal is the form of the mouth region and of the branchial pouches, features so seldom seen that the great majority of species (there are some ninety described) 'ne peuvent . . . être actuellement rattachées à un genre', while 'Le génotype de *Cephalaspis*, *C. lyelli* Agassiz, a une chambre oralobranchiale mal conservée et il est par suite peu probable qu'on puisse jamais définir et détérminer à quel orde il appartient'.

Stensiö's remarks regarding the condition of the oralo-branchial chamber of *C. lyelli* are not applicable. While it is true that at the moment there is only one specimen known of this species, there is no reason why others should not be found, and what he says of the unique lectotype is fortunately not now correct and, whether one accepts Stensiö's new classification or not, it is possible to determine the position of *Cephalaspis* in it, and to say which of his genera is its synonym.

HISTORY OF THE SPECIES

The genus *Cephalaspis* was described by Agassiz in 1835 (p. 135, pl. 1*a*, 1*b*) and to it were assigned four species, *C. lyelli*, *C. rostratus*, *C. lewisi*, and *C. lloydi*. The last two were removed by Kner in 1847 to form the types of a supposed cuttlefish *Pteraspis*, and in 1858 T. H. Huxley showed that they were the ventral plates of a species of 'fish' of which *Cephalaspis rostratus* was the dorsal armour, leaving *C. lyelli* as the only original species of *Cephalaspis*, and therefore the type species.

As was usual at that time Agassiz based his description of the species on an indeterminable number of specimens from Scotland and England of which he figured five (pl. 1*a*, figs. 1 and 2; pl. 1*b*, figs. 1, 3, 5). The last specimen, which looks like a piece of a pteraspid, is apparently lost, so that the other four figured specimens are the only ones now identifiable and are therefore the only effective co-types.

[Palaeontology, Vol. 1, Part 2, 1958, pp. 99–105, pls. 18–19.]

Forty-five years later Ray Lankester (1870, p. 43, &c.) redescribed these co-types, and removed three out of the four to other new species, the originals of Agassiz's pl. 1*a*, fig. 1 and pl. 1*b*, fig. 1 to *C. powriei*, and of pl. 1*b*, fig. 3 and all other English specimens to *C. agassizi*, leaving the specimen figured in pl. 1*a*, fig. 2 as the lectotype, by elimination, of *C. lyelli*. This famous specimen, which was given to the British Museum in 1846 by Sir Charles Lyell himself, was refigured by Lankester (pl. 8, fig. 1) in a much improved representation by Mr. Dinkel, the same artist who had drawn Agassiz's original figure thirty-five years before. In the meantime the specimen had undergone considerable change; much of the tail had been uncovered and so had the lower part of the body-scales especially of the right side, but in clearing the sides from the matrix, which is a hard coarse sandstone, most of the pectoral paddles had been destroyed. It is, however, from Agassiz's original figure that the representation of this specimen in Murchison's *Silurian System* (1839, pl. 1, fig. 2), in the various editions of *Siluria* (e.g. 5th edit., 1850, pl. 37, fig. 1) and in numerous textbooks to the present day, have been taken.

Lankester added another specimen, from Arbroath, to the species (1870, pl. 11, figs. 1, 2) but even in its imperfect state it seems too wide in the head, and to have too few rows of body-scales, to be conspecific. He also published a rather primitive restoration of the species (text-fig. 16, p. 41).

Woodward (1891, p. 179) reunited the English specimens described as *C. agassizi* with *C. lyelli*, but he did not figure the type-specimen (No. 20087), but contented himself with reproducing Lankester's restoration. Curiously enough he did not notice that a second, fragmentary specimen (P. 3233), which he described as 'Portions of head and trunk of similar specimen; Glammis', was in fact part of the counterpart of the lectotype. Somehow it had become separated from the major specimen and came to the Museum in the Earl of Enniskillen's great collection in 1882, thirty-six years after the other part.

Stensiö (1932, p. 119, text-fig. 40, pl. 15, fig. 1), in his distinguished work on the British Cephalaspids, gives a very restricted account of the species. He was unable to figure the lectotype as it was then not possible for the specimens to leave London, and the counterpart as then developed added little or nothing to the known details. He stated that 'The exoskeleton of the cephalic shield is much weathered and therefore not in a condition for detailed study'. In fact the specimen was not weathered at all, but when the counterpart was split off it left, for the most part, only the basal layer on the major specimen, while the details of the counterpart were obscured by the other bony layers. Stensiö tentatively placed in the species (1932, pl. 15, fig. 1) specimens from Brechin, which are now shown clearly to be unrelated. Possibly they belong to a form of *C. powriei*.

DESCRIPTION OF LECTOTYPE

The main portion (B.M. No. 20087), that described and figured by Agassiz and others, consists of an almost complete animal, virtually an internal cast. The cornua show only the bone of the underside. The paddles are now badly mutilated. The extreme tip of the snout is damaged and about half of the tail is missing, doubtless removed when the block of sandstone was originally trimmed, for the whole of the tail at this time was covered in matrix and its presence unsuspected. The specimen is not quite symmetrical, for the right side has been slightly crushed, as the dorso-lateral scales show, but the left side is almost undistorted.

The counterpart (B.M. No. P. 3233), now in the form of an external mould, comprises only part of the right side from the level of the front of the orbit to the spine of the (posterior) dorsal fin. The cast shows to some extent the condition of the original specimen in Agassiz's time, for the pectoral paddle is present, but only part of the cornu shows and none of the ventro-lateral scales or the tail. Fortunately the central area of the shield with the cephalic spine and the ridge scales and dorsal fin are well preserved.

The main specimen and counterpart will be described together.

As preserved the specimen measures 20·5 cm. in length. The complete animal measured about 24·5 cm., as can be judged by comparison with a specimen of *C. pagei* figured twice natural size by Stensiö (1932, pl. 35, fig. 3), for the two figures coincide closely in the length of the head-shield, and in the position of dorsal fin and the root of the tail.

The length of the cephalic shield to the tip of the brief spine is about 8·0 cm., almost exactly one-third of the animal's total length, and the maximum breadth, across the posterior part of the cornua, a little less, about 7·8 cm. The breadth narrows forwards and the front of the shield was almost certainly rounded. The distance of the front margin to the pectoral sinus is on average 6·7 cm., and to the tips of the cornua 9·5 cm., so that the cornua were about 2·8 cm. long. The interzonal part at its posterior end is 3·4 cm. broad, less than half the maximum breadth of the shield. The maximum height, at the base of the dorsal spine, is now 1·5 cm., but was probably nearly 2 cm. since the cornua, especially on the right side, are bent upwards. There are no denticles on the inner margin of the cornua but there seems to have been a small but distinct pectoral angle.

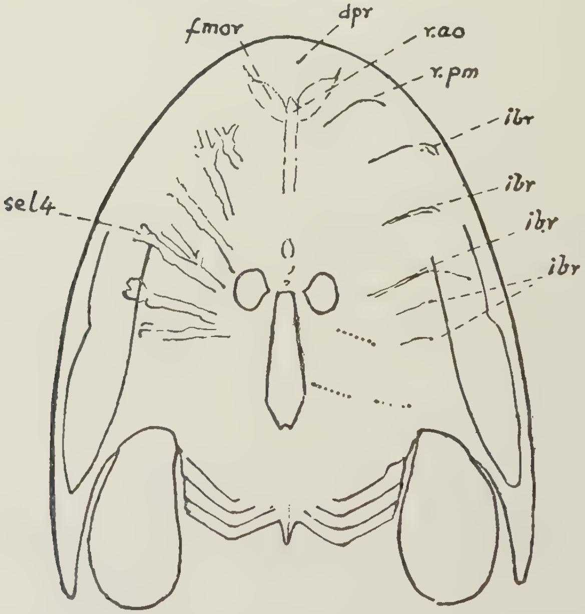
The interzonal part is short and to it is attached one undivided scale-row, while two others are incompletely separated from the base of the spine on each side. It bears a low but well-defined crest ending in a short, hooked, laterally compressed spine.

The orbits are oval, of moderate size, 0·65 cm. long and 0·45 cm. wide with an inner median projection. They lie at the middle of the length of the shield measured from the tip of the snout to that of the dorsal spine and are thus much nearer the pectoral sinuses than to the front margin. The position of the hypophyseal sac is clearly indicated in front of the orbits. The median dorsal sensory field is very well preserved in impression in the counterpart and is most distinctive in shape. It is very long and narrow. The length is 2·2 cm. with perfectly straight sides diverging gradually to the rear, the breadth being only 0·3 cm. at the front margin and increasing gradually to 0·7 cm. at a point 0·4 cm. from the hinder end. It then narrows rapidly to 0·2 cm. in front of the dorsal spine where it ends with a slight re-entrant angle. The hinder two-thirds of the right lateral field is similarly preserved. It runs well on to the cornu, for about 1 cm. and ends in a blunt point. The field is relatively broad, about 0·8 cm. at its maximum. The marked notch on the outer margin is very probably an individual defect.

As Stensiö (1932, p. 121) has noted, the endoskeleton is imperfect but at least some of the perichondrial bone-layers were present, such as the orbital and labyrinth layers and those which lined the canals of the lateral sensory fields; but on the whole the skull was very lightly ossified. A fair proportion of each of the six sensory canals can be seen on the left side, and, more obscurely, parts of the other vessels as well.

The supra-oral field (*dpr*), roughly triangular in form, is very faint, without a transverse ridge, and extends only a short distance to the aortic ridge (*r.ao*), and the paratoral depressions (*f.mor*) are likewise inconspicuous and virtually absent. Most important are the clear indications of the pre-branchial (*r.pm*) and inter-branchial ridges which by their obliquity clearly indicate that the species falls within Stensiö's group Oligobranchiata, while the form of the oral area places it within his family Zenaspidae. *Cephalaspis* is identical with Stensiö's *Zenaspis*, as one might have expected by its general form.

The right pectoral limb is well preserved as an impression in the counterpart. It is paddle-shaped with a rounded contour, measuring 2·9 cm. in length and 1·7 cm. wide at the maximum. Faint indications of overlapping scales are shown, chiefly near the outer margin.



TEXT-FIG. 1. Head-shield and pectoral paddles of the lectotype. Slightly restored. $\times\frac{4}{5}$. *dpr*, supra-oral field; *f.mor*, paratoral field; *ibr*, inter-branchial ridges; *r.ao*, aortic ridge; *r.pm*, pre-branchial ridge.

The cast of the counterpart shows that the superficial layer of the exoskeleton was continuous and the surface unornamented, the fine irregularities to be seen being due to the coarseness of the matrix. The mucous canal system was entirely enclosed in the exoskeleton. Only here and there are the tesserae of the sensory fields to be detected.

Indications of two pit-lines are visible, *cm* and cmm_1+cmm_2.

None of the exoskeleton of the oralo-branchial region on the undersurface is preserved.

The trunk is exposed except the undersurface (which indeed appears to be absent) and

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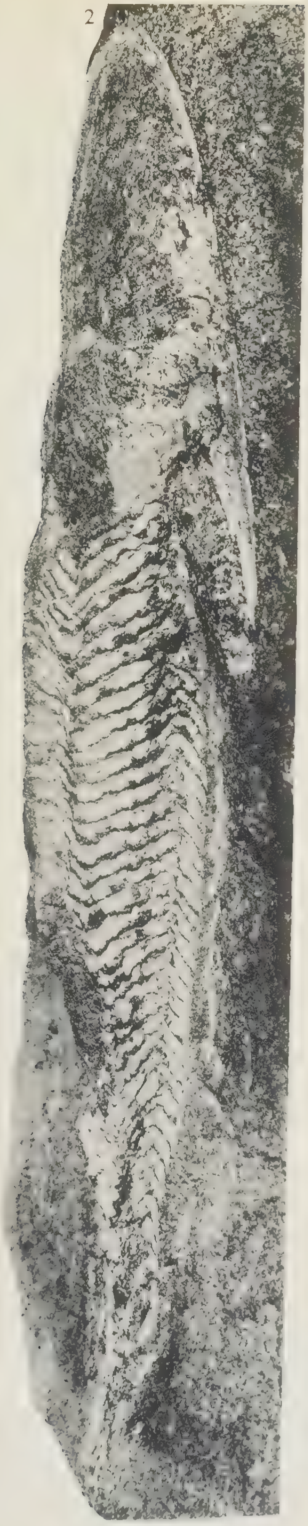
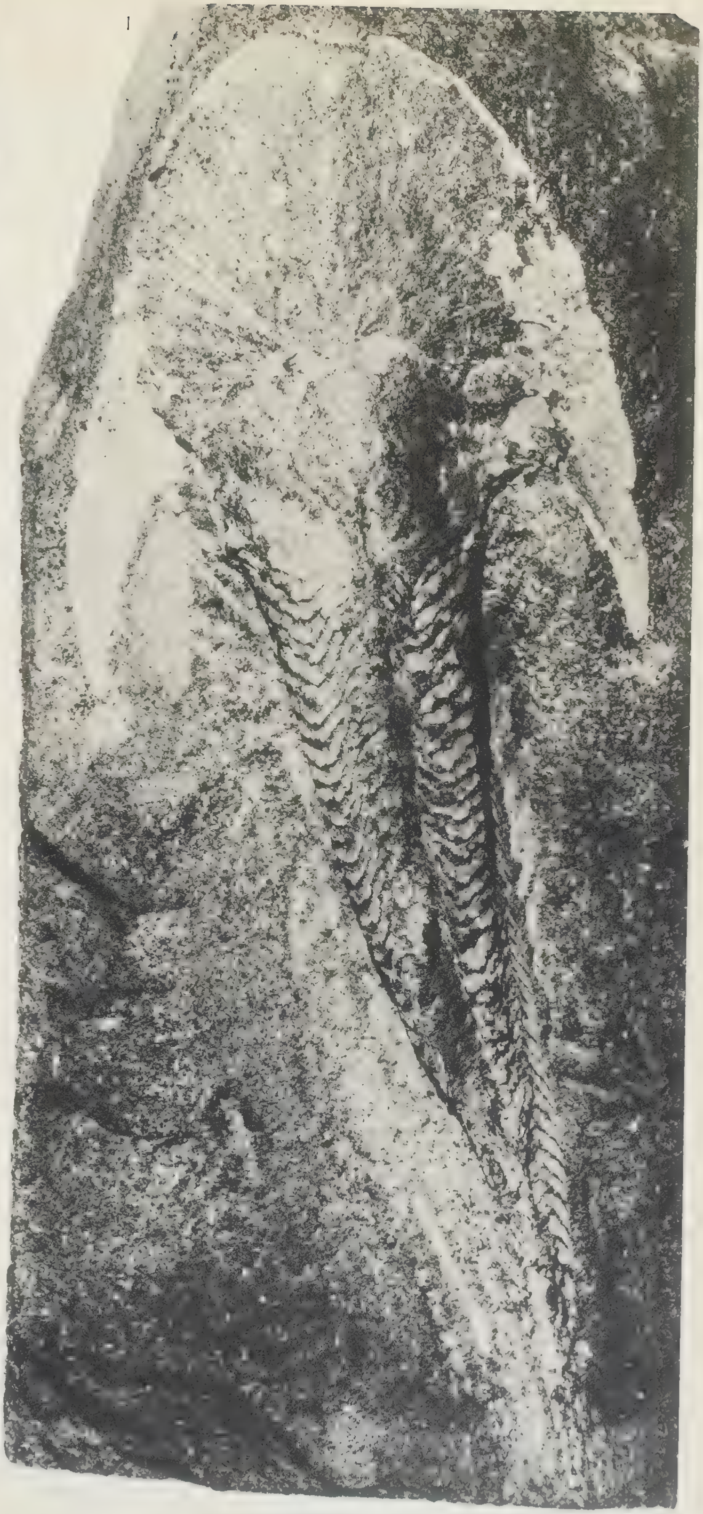
EXPLANATION OF PLATE 18

Figs. 1–2. *Cephalaspis lyelli* Agassiz. 1, The lectotype, dorsal view. The specimen is 20·5 cm. long. The ridge-scales are missing. Lower Old Red Sandstone, Glamis, Angus, Scotland. B.M. (N.H.) No. 20087. 2, The same specimen, side-view.

2

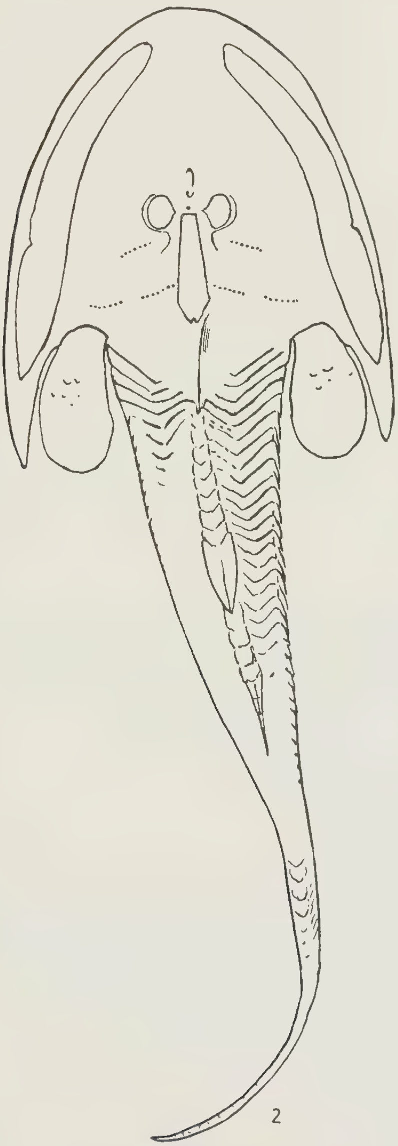


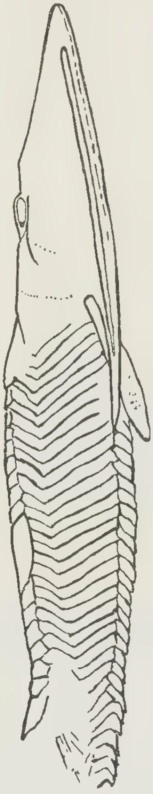
1



WHITE, *Cephalaspis lyelli*

the lower part of the left side, which is still covered in matrix. In form the body is triangular with well-rounded sides. It was about 3·0 cm. high and 3·5 cm. wide at the base in front, immediately behind the interzonal part. It decreases rather rapidly both in





TEXT-FIG. 2. *Cephalaspis lyelli.* Outline of complete animal. × $\frac{2}{3}$.
TEXT-FIG. 3. *Cephalaspis lyelli.* Head and body, side view. × $\frac{2}{3}$.

eight and breadth towards the tail. The animal was therefore a good deal flatter than in *Iemicyclaspis* (cf. Stensiö 1932, text-fig. 15, p. 53), but the form of the squamation was ssentially the same. There are, however, important differences, of which the more obvious are that there are far fewer rows of scales with broader and shallow flank-scales, and that the flank-scales and dorso-lateral scales were fused together.

Including the three partially fused rows in front there are thirty-seven scale-rows to the root of the tail, as against some fifty-five in *Hemicyclaspis*. The fused dorso-lateral and lateral scales form a conspicuous angle with one another (somewhat exaggerated by crushing in Pl. 18, fig. 2) since the former slope backwards and the latter forwards, the angle in the middle of the body being about 90°, becoming slightly greater in front and increasingly more acute towards the tail. The scales of course overlap one another backwards, the breadth of the exposed surface of the larger scales being rather less than 0·3 cm. on the slightly concave right side and rather more on the convex left side. The breadth of the overlapped area is uncertain. The height along the scale of the dorso-lateral part is 1·1 cm. at about the ninth scale, that of the main lateral scales about twice as high. The main lateral part of the scales decreases rapidly at the level of the hinder end of the enlarged dorsal ridge-scale, that is from about the twentieth row, and at the level of the twenty-seventh under the dorsal fin, the dorso-lateral parts break up into a mosaic.

The azygous row of A-shaped ridge-scales again slopes backwards more or less parallel with the main lateral portions, forming a similar angle with the dorso-lateral parts, but they are much lower, being only 0·4 cm. in height. They do not correspond with the scale-rows, being broader, about 0·35 cm. There are nine from the sixth scale-row, that immediately behind the cephalic spine, to the sixteenth. From the seventeenth to the twenty-second rows there is a single large ridge-scale, representing the remains of the anterior dorsal fin, and then three rather long ridge-scales corresponding to scale-rows 23–27 immediately followed by the spine of the dorsal fin. The spine is deep and pointed, formed by three distinct pieces, much laterally compressed. No part of the fin itself is preserved but the series of ridge-scales behind it starts over scale-row 36 and gradually diminishing in size continues as far as the specimen is preserved.

The tail is very crushed, although much of it is now free from the matrix. The scales on the axis were very small and arranged obliquely upwards and backwards, much as in *Hemicyclaspis*.

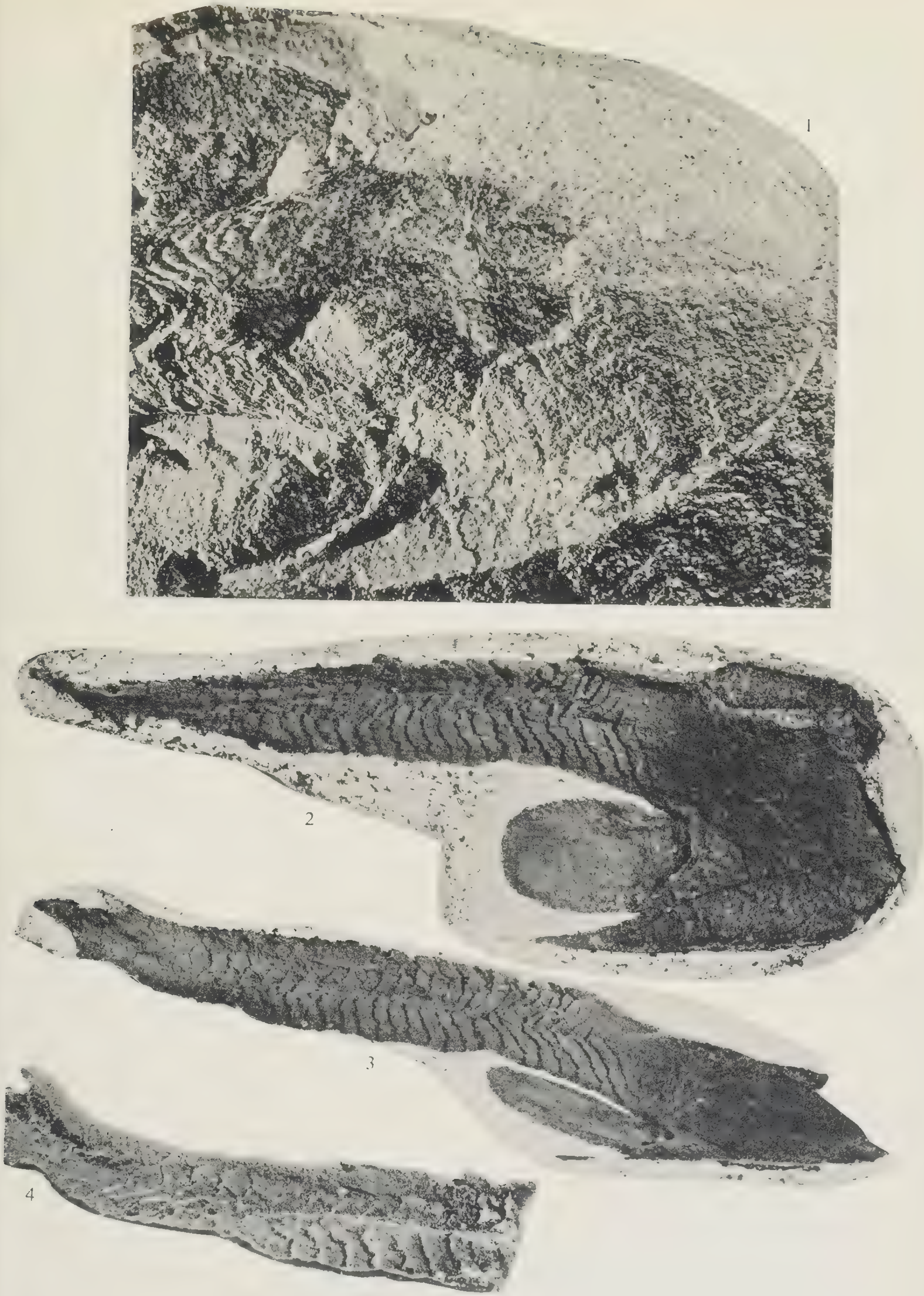
The ventro-lateral series of scales, exposed only on the right side, correspond with the scale-rows, but are separate from the lateral scales, with which they form the same sharp angle as the other series do with one another. The largest are 6·0 cm. in height and end in a free point directed ventro-laterally. They continue right to the base of the tail.

As noted above, none of the undersurface of the body is exposed, and it would appear, from trial excavations, that the ventral scales, which form most of the under surface, and those covering the oralo-branchial chamber, have been lost.

This species has several characteristic features that distinguish it from other British forms. The straight-sided, narrow median sensory field is unique, and none has such markedly zigzag scale-rows, nor completely undivided dorso-lateral and lateral scales.

EXPLANATION OF PLATE 19

Figs. 1–4. *Cephalaspis lyelli* Agassiz. 1, Cephalic shield of lectotype, showing cast of oralo-branchial chamber; for explanation see text-fig. 1. Slightly enlarged. 2, Cast of imperfect counterpart of lectotype, dorsal view. Approximately natural size. B.M. (N.H.) No. P. 3233. 3, The same specimen, side view. 4, Another cast of part of the same specimen showing the enlarged ridge-scale and the spine of the dorsal fin (scale-rows 15–30 approx.). ×1½.



WHITE, *Cephalaspis lyelli*

That the form of the scale-rows is not wholly due to distortion is shown by the form of the back of the cephalic shield with which they are parallel, but it is not certain whether the undivided state of the dorsolateral parts of the body-scales is a specific character or the normal condition in the genus, the apparent subdivision of those parts in other species being the result of cracking after death across lines of weakness due to the venous sinuses; but it is clear that they are not regularly formed as restored in *Hemicyclaspis* by Stensiö (1932, text-figs. 15, 23).

From being one of the least-known species of cephalaspid, *Cephalaspis lyelli* is now in many respects as well known as any, but the important result of this study is to show its position in Stensiö's new arrangement of the group, and its identity with *Zenaspis*.

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BRITISH UPPER SILURIAN CRINOIDS FROM THE LUDLOVIAN

by W. H. C. RAMSBOTTOM

ABSTRACT. A brief review of the crinoid fauna of the Ludlow formation is followed by the redescription of *Eutaxocrinus maccoyanus* (Salter) and *Meristocrinus orbignyi* (M'Coy). The following new species are described: *Gissocrinus ludensis, Mastigocrinus bravoniensis,* and *Hapalocrinus quinquepennis*. *Pisocrinus* cf. *sphericus* (Rowley) and *Cicerocrinus spp.* also occur in the fauna.

INTRODUCTION

'STARFISH BEDS' are a well-known feature of the Ludlovian in Britain. Associated with the starfish in these beds are crinoids, often numerous in individuals if not in species, and these have hitherto not received much attention. The crinoid faunas of the starfish bed at Church Hill, Leintwardine, Herefordshire, and of another such bed near Kendal, Westmorland, are here described, and the opportunity is taken to review briefly the whole crinoid fauna of the Ludlovian in Britain.

Crinoids occur at two principal horizons in the Lower Ludlow. In the *Monograptus nilssoni* Zone '*Actinocrinus*' *pulcher* M'Coy, which is probably referable to the genus *Scyphocrinites,* is widespread in north and mid Wales and extends into the Lake District at what is possibly a similar horizon. In Ireland this species may be represented by *Actinocrinus wynnei* Baily (1860), but the type specimens of this latter species have not been available for examination. *Scyphocrinites* is also known in Cornwall (Bather 1907), but although possibly of Ludlovian age the precise horizon is uncertain. The species of *Scyphocrinites* found in Cornwall is more closely related to the species from Bohemia than to *S.? pulcher* in the Anglo-Welsh area, and this fact has palaeogeographical significance. British examples of *Scyphocrinites* will form the subject of another paper.

At the higher horizon of the *Monograptus leintwardinensis* Zone lagoonal conditions at Leintwardine (Hawkins and Hampton 1927) allowed the preservation of a considerable number of specimens though only six species are represented. Two of these (*Eutaxocrinus maccoyanus* and *Hapalocrinus quinquepennis*) are also represented in Westmorland at a similar horizon, together with another species, *Meristocrinus orbignyi,* unique to that district. Mr. E. V. Tucker has collected a fragmentary *Periechocrinus* (GSM Zl 7053) from 10 feet below the base of the equivalent of the Aymestry Limestone in a lane section south of Perton, Herefordshire.

In the Upper Ludlow the only known crinoids belong to *Cicerocrinus,* also found in Sweden and the south Baltic area at a similar horizon, but the information available as to the occurrence of this genus is not altogether satisfactory.

When compared with the prolific crinoid life of the earlier Wenlock Limestone the evidence in Britain is of an impoverished fauna, probably due to the onset of unfavourable conditions. But the Ludlow crinoids seem to be in part transitional to the extensive Devonian faunas, for three of the seven genera (*Hapalocrinus, Eutaxocrinus,* and *Scyphocrinites*) are better represented in the Devonian than in the Silurian.

[Palaeontology, Vol. 1, Part 2, 1958, pp. 106–115, pls. 20–21.]

Most of the specimens described in this paper occur as external moulds and they have been studied by means of rubber latex casts prepared with Revultex supplied by Revertex Ltd., London.

Acknowledgements. I am indebted for the loan of specimens to the Directors of the British Museum (Natural History) [BM] and of the Geological Survey and Museum [GSM], to Mr. J. M. Edmonds of the University Museum, Oxford [OM], to Dr. F. Hodson of Reading University, and to Mr. A. G. Brighton of the Sedgwick Museum, Cambridge [SM]. The letters in brackets are those used to distinguish the registered numbers of specimens in the various institutions.

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SYSTEMATIC DESCRIPTIONS

Sub-class FLEXIBILIA Zittel

Genus MERISTOCRINUS Springer 1906

Type species by original designation: *Cyathocrinus interbrachiatus* Angelin, Silurian, Gotland.

Diagnosis. A genus of Sagenocrinitidae with the radianal in the form of a radial beneath the right posterior radial. Interbrachials few or none, followed by perisome. Primibrachs three.

Meristocrinus orbignyi (M'Coy)

Plate 20, fig. 7

Taxocrinus? Orbignyi M'Coy 1850, p. 289.
Taxocrinus? Orbignyi M'Coy 1851, p. 53, pl. 1*d*, fig. 1.
Meristocrinus orbignyi Springer 1906, p. 519.
Meristocrinus orbignyi Springer 1920, p. 213, pl. 17, fig. 7.

Holotype. SM A 29599.

Occurrence. Lower Ludlow, Bannisdale Slates, *Monograptus leintwardinensis* Zone (*fide* Marr 1892, p. 538), 'Asterias Bed', High Thorns, Underbarrow, Kendal, Westmorland. The holotype is the only known specimen.

Diagnosis. A species of *Meristocrinus* with the stem not expanding towards the cup, and in which the brachials have a slight distal expansion.

Description. Cup bowl-shaped with subparallel sides, surface of cup plates smooth. Infrabasals low, appearing in side view like an enlarged columnal. Basals one-third the height of the radials, much wider than high, the facets occupying the whole width of the plates. Primibrachs three, wider than high; secundibrachs five. Arms dividing three times isotomously, though in the distal region the divisions are not at the same height in each branch. Proximally the brachials are wider than high, but distally they become as high or even higher than wide. Brachials have a slight distal expansion or cornice on their dorsal sides. Posterior side of cup not seen, but traces of the interbrachial perisome of tiny plates are seen in one interbrachial area. Tegmen not seen. Stem round, large, not expanding towards the cup, formed of uniform, ridged, short columnals with crenellate surfaces; preserved for a length of 33 mm.

Discussion. The unique holotype is preserved as an external mould in sandstone, and only the anterior side of the cup is seen. Some development of the specimen has been possible and a good Revultex impression has been made. The reference of the species to *Meristocrinus* is largely based on the presence of three primibrachs, a rare feature in Silurian Flexibilia, but also on the form of the crown.

The figure given by M'Coy (1851) and reproduced by Springer (1920) is very much restored and is inaccurate in several respects. The basals in that figure are too big, the infrabasals are not shown, no sign of the interbrachial perisome appears, and the arm branching is too artificial and regular. The species is well characterized by the distal expansions on the brachials and the non-expanding stem.

The horizon of this species was given, in error, as Upper Ludlow by M'Coy. The stratigraphical position of the Starfish Beds in the Bannisdale Slates has been commented on by Marr (1892, p. 539), but in which of several Starfish Beds the crinoids occur is not known.

Genus EUTAXOCRINUS Springer 1906

Type species by original designation: *Taxocrinus affinis* Müller, Middle Devonian, Germany.

Diagnosis. A genus of Taxocrinidae with the rays not abutting over the interbrachials; infrabasals low; posterior basal elongate; radianal usually absent; few or no interbrachials; primibrachs two.

Eutaxocrinus maccoyanus (Salter)

Plate 20, figs. 4–6

Ichthyocrinus pyriformis M'Coy 1851, p. 54.
Ichthyocrinus McCoyanus Salter 1873, p. 163.
Taxocrinus La Touche 1884, pl. 17, fig. 551.
non *Ichthyocrinus pyriformis* (Phillips 1839).

Holotype. SM A 35407.

Occurrence. The holotype is from the Lower Ludlow, Bannisdale Slates, *Monograptus leintwardinensis* Zone (*fide* Marr 1892, p. 538), 'Asterias Bed', Light Beck, Underbarrow, Kendal, Westmorland. Two specimens are known from a similar horizon at Church Hill Quarry, Leintwardine, Herefordshire (BM E 26578, GSM 89989), and one specimen (GSM 89988) is labelled 'Underbarrow' and may be from the same locality as the holotype.

Diagnosis. A species of *Eutaxocrinus* without interbrachials, with three or four secundibrachs, arms branching isotomously, brachials smoothly rounded on their dorsal sides and smooth cup plates.

Description. Cup low, wider than high, surface of cup plates smooth. Infrabasals and basals of about equal height, very low and much wider than high. Radials form the height of the cup, slightly wider than high with the facets occupying the full width of the plates. Primibrachs two; secundibrachs three or four; arms dividing isotomously three times. All brachials wider than high, smooth and with rounded dorsal sides. Posterior side of cup not seen. Interbrachials absent. Stem widens slightly proximally and there is formed of low columnals, the first twelve or thirteen being of uniform size. Distally there is an irregular alternation of longer and shorter columnals. Surface of columnals crenellate.

Discussion. No mention of this species is made by Springer (1920). Though the posterior side of the cup has not been seen, the species is referred to *Eutaxocrinus* with some confidence, for the form of the crown is characteristic. This species is the earliest, stratigraphically, so far known, of the more typical members of the genus, since *E. oblongatus* (Angelin) from the Silurian of Gotland is not at all typical in its arm branching. *E. maccoyanus* is mainly characterized by the low cup and smooth surface of the cup plates and brachials; *E. rhenanus* (C. F. Roemer) from the Devonian of Germany is perhaps the species which it most resembles.

Salter (1873) spelt the specific name '*McCoyanus*'. This has been altered to *maccoyanus*, an emendation in accordance with current recommendations (see *Bull. Zool. Nomencl.* **14,** 198).

Three of the four known specimens are figured on the plate. One of those (Pl. 20, fig. 6) from Leintwardine is apparently that figured by La Touche (1884, pl. 17, fig. 551), which was formerly in the Ludlow Museum but now housed in the British Museum (Natural History). Another (unfigured) Leintwardine specimen is notable in being the only specimen examined from that locality in which the actual plates are preserved in calcite (GSM 89989), though the sutures are somewhat obscure in places.

Sub-class INADUNATA Wachsmuth and Springer
Order CLADOIDEA Moore and Laudon
Genus GISSOCRINUS Angelin 1878

Type species by subsequent designation of Ramsbottom (1951): *Actinocrinites? arthriticus* Phillips, Wenlock Limestone, Dudley.

Diagnosis. A genus of Cyathocrinitidae with three infrabasals.

Gissocrinus ludensis (Sollas MS.) sp. nov.

Plate 21, figs. 8–9

Holotype. BM E 26573. *Paratype.* BM E 26577.

Occurrence. All the known specimens come from the Lower Ludlow Beds (*Monograptus leintwardinensis* Zone) at Leintwardine, Herefordshire. The British Museum specimens, including holotype and paratype, come from Church Hill Quarry, Leintwardine.

Diagnosis. A species of *Gissocrinus* in which the cup is cone-shaped with strong axial ridges. Infrabasals about the same height as the basals; brachials round backed; stem nodose, subpentagonal distally, round in the proximal few millimetres.

Description. Cup narrow, cone-shaped, higher than wide, with strong axial ridges. Infrabasals about as high as the basals, which are about as high as wide. Radials about as high as wide, the facet occupying about one-third of the width of the plate. Primibrachs three; arms branch about five times, the brachials being round backed and usually higher than wide and without distal expansion or ornament of any kind. Four covering plates per brachial. Anal tube formed of squarish plates with fine but deep transverse folds; tube about the same length as the arms. Tegmen not seen. Stem, seen to a length of 60 mm., round in the proximal few millimetres, afterwards subpentagonal; formed of alternating nodals and internodals, with larger nodals situated at intervals.

Discussion. Among the species of *Gissocrinus* from the Wenlock Limestone of Dudley it is only with *G. scoparius* (Salter) that this species shows any close relationships. The features of theb rachials, the shape of the cup, and the large size of the infrabasals distinguish this species. The subpentagonal stem is also characteristic. The specimen to which Sollas attached the manuscript name *ludensis* on a museum label (OM c 85) is a young specimen, the crown being only 12 mm. in height. In view of this a more adult example has been chosen as the holotype, and in this the crown has a height of 50 mm. All the specimens are preserved as external moulds, as is usual at Leintwardine.

Genus MASTIGOCRINUS Bather 1892

Type species by monotypy: *M. loreus* Bather, Wenlock Limestone, Dudley.

Diagnosis. A genus of Botryocrinidae in which the radianal is absent. Anal plate in line with radials. Arms long, isotomously branched, non-pinnulate. Anal tube long, flattened, and with strongly folded plates. Tegmen formed of many small plates. Stem divided longitudinally into pentameres.

Mastigocrinus bravoniensis sp. nov.

Plate 21, figs. 6–7

Holotype. GSM 89994. *Paratype.* OM c 84.

Occurrence. All known specimens are from the Lower Ludlow Beds (*Monograptus leintwardinensis* Zone), Church Hill Quarry, Leintwardine, Herefordshire.

Diagnosis. A small species of *Mastigocrinus* in which the brachials are higher than wide. Primibrachs usually four, sometimes five.

Description. A small species; cup conical, about as wide as high, surface of cup plates smooth or slightly granular. Infrabasals occupy a quarter of the height of the cup; basals occupy half the height of the cup and are as wide as high; posterior basal truncate and considerably wider than the others. Radials a little wider than high, occupying one-third of the height of the cup; radial facets occupying the whole width of the radials. Primibrachs usually four, sometimes five, slightly higher than wide. Arms branch three or

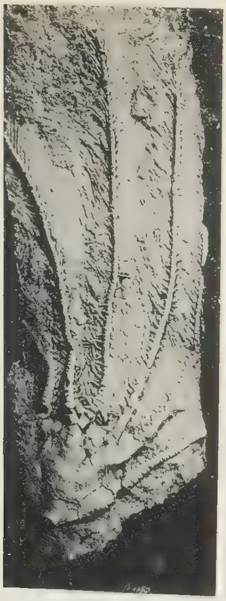
EXPLANATION OF PLATE 20

All photographs are of rubber latex (Revultex) casts coated with ammonium chloride.

Figs. 1–3. *Hapalocrinus quinquepennis* sp. nov. Lower Ludlow, Leintwardine, Herefordshire; figs. 2 and 3 from Church Hill Quarry. $\times 1\frac{1}{2}$. 1, holotype, BM E 26576a. 2, paratype, GSM 89897. 3, paratype, BM E 14900.

Figs. 4–6. *Eutaxocrinus maccoyanus* (Salter). Lower Ludlow. 4, holotype, SM A 35407, × 3, Bannisdale Slates, Light Beck, Underbarrow, Westmorland. 5, GSM 89988, × 3, Bannisdale Slates, Underbarrow. 6, BM E 26578, × 2, Church Hill Quarry, Leintwardine, Herefordshire.

Fig. 7. *Meristocrinus orbignyi* (M'Coy). Lower Ludlow, Bannisdale Slates, High Thorns, Underbarrow, Westmorland. Holotype, SM A 29599, × 2.



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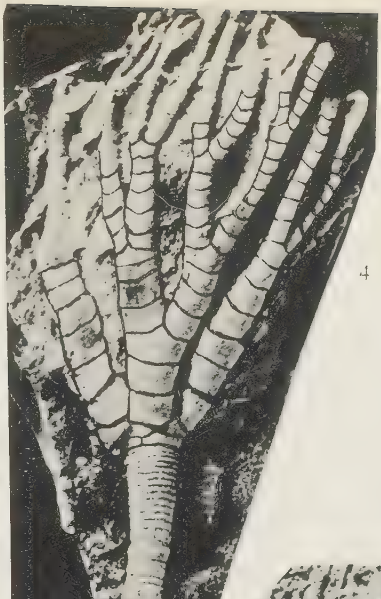

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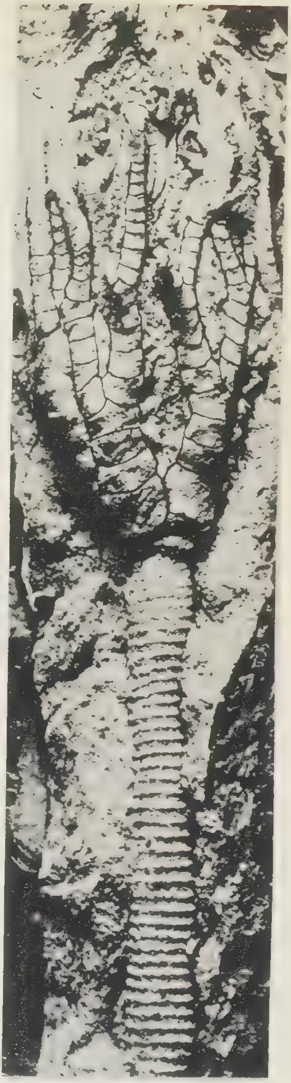

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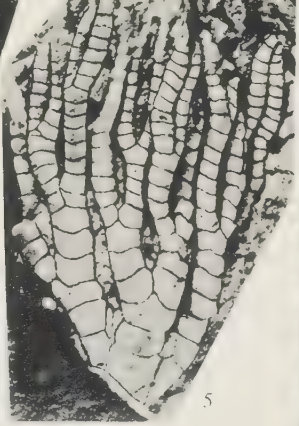

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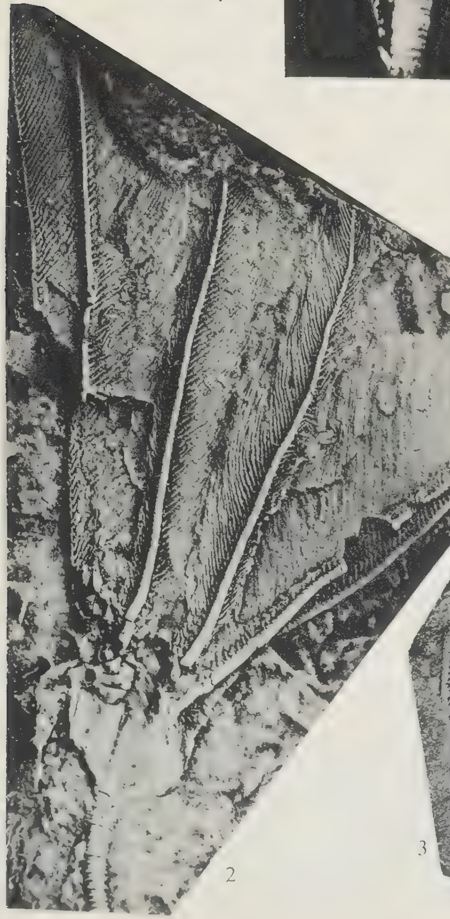

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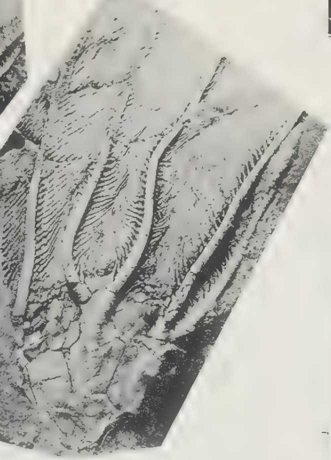

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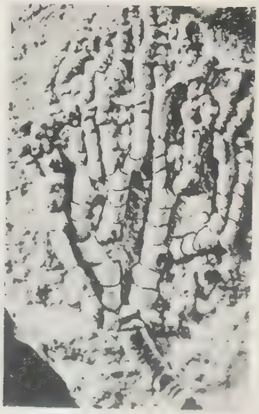

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RAMSBOTTOM, Ludlovian crinoidea

possibly four times isotomously; brachials with evenly rounded dorsal sides; axial canal and food groove confluent. Anal plate relatively large, considerably wider than high; anal tube formed of rectangular plates which are folded longitudinally, and there are in addition transverse folds of the same type as in *M. loreus* (Bather 1892). Stem slightly subpentagonal, smooth, formed of alternating thin and thick columnals.

Discussion. It was at first thought that this small species, represented by a number of external moulds from Leintwardine, belonged to *Cyathocrinites* and Sollas had so labelled the paratype in the University Museum, Oxford. The posterior side and anal tube are exposed in the holotype, however, and they show that it should be referred to *Mastigocrinus*. It is easily distinguished from *M. loreus*, the only other described species of the genus, by the length of the brachials and the small size. The specific name is derived from the Roman name for Leintwardine.

Order DISPARATA Moore and Laudon
Genus CICEROCRINUS Sollas 1900

Type species by monotypy: *C. elegans* Sollas, unlocalized, probably Upper Ludlow.

Diagnosis. A genus of Pisocrinidae with an elongate cup which is confluent with the stem, branched pinnulate arms, and radials without pronounced lateral processes.

Cicerocrinus elegans Sollas

Plate 21, figs. 2–5

Cicerocrinus elegans Sollas 1900, p. 267, pl. 16, figs. 3–4.
Lagarocrinus tenuis Jaekel 1900, p. 487.

Holotype. OM c 80.

Occurrence. The holotype is unlocalized. Sollas suggested that it was Wenlock in age, but its mode of preservation is unlike that of any other Wenlock crinoid examined. It is here suggested that its age is more probably Upper Ludlow on account of the matrix and mode of preservation, which accords well with that of other Upper Ludlow crinoids, and because all other examples of the same species are of Upper Ludlow age.

Specimens have been examined from the Upper Ludlow, Whitcliffe, Ludlow, Shropshire (BM E 26071a); quarry near old bridge, Ludlow (BM E 5726—holotype of *C. tenuis* —here figured plate 21, fig. 3); small roadside quarry, 150 yards north of Stapleton Castle, Stapleton, near Presteigne, Radnorshire (GSM 85405); old quarry 150 yards east-north-east of Warren House Farm, *c.* 2 miles from Knighton on the Knighton to Penybont road (GSM 85406).

Diagnosis. A species of *Cicerocrinus* in which the cup is about twice as high as wide; pinnules are borne usually on every fourth brachial.

Description. Cup conical, about twice as wide as high, surface of cup plates smooth. Basals half the height of the radials. Radials without marked lateral processes, facet occupying the whole width of the plate. Primibrachs two, the first being about twice as wide as high, the second usually higher than wide. Secundibrachs up to twenty observed; tertibrachs up to twenty-eight observed. In adult (i.e. large) specimens the arms branch twice, but in small specimens only once; all brachials variable in height, being up to twice as wide as high or twice as high as wide. Pinnules are borne on secundibrachs and tertibrachs usually occurring on every fourth brachial, but sometimes three and sometimes five brachials occur between divisions. Sutures of the pinnule-bearing brachials are at an angle with the sides of the arm. Pinnulars longer than wide, tapering sharply, and with a relatively wide proximal end. Small anal plate, but no tube has been seen in the available material. Tegmen not seen. Stem round, smooth, expanding proximally and confluent with the base of the cup.

Discussion. The specimen described by Sollas is unique in being so well preserved, and all the other specimens are more or less fragmentary. It is thought, however, that all the English Upper Ludlow *Cicerocrinus* specimens are conspecific with this fine specimen. *C. anglicus* (Jaekel) may be an exception (see below). In the case of *C. tenuis* (Jaekel), the holotype is a young specimen in which the arms divide only once, but it otherwise shows no differences which would suggest that it would not have grown up into a typical *C. elegans*. The suggestion of an Upper Ludlow age for the holotype of *C. elegans* seems unavoidable.

Cicerocrinus anglicus (Jaekel)

Lagarocrinus anglicus Jaekel 1900, p. 486.

Original description. 'Oberes Obersilur (Low. Ludlow beds). Gomey Quarry, Presteigh, Radnorshire in Süd Wales, England. Hohe des Kelches etwa 20 mm., Länge der Arme etwa 34 mm. Arme zunächst in 10 gleichwertige Hauptäste getheilt, diese mit zahlreichen (etwa 24), aber anscheinend ziemlich kurzen Ramulis versehen. Stiel oben beträchtlich erweitert, namentlich in die Dicke des Kelches übergehend. 1 Orig.-Ex. Museum f. Naturkunde, Berlin.'

Discussion. I am informed by Professor W. Gross that the holotype of this species has disappeared from the Museum für Naturkunde in Berlin. Since no topotype material has been available it has not been possible to make a proper study of this species, for there is no figure. The description would suggest a distinct species characterized by many pinnules.

The horizon and locality of the holotype are in doubt. There is no place in Radnorshire with the name 'Presteigh' as given by Jaekel, and it is probable that Presteigne was intended. Modern maps do not mark any place called 'Gomey', and the nearest to this is

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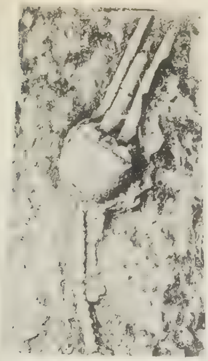
EXPLANATION OF PLATE 21

Fig. 1. *Pisocrinus* cf. *sphericus* Rowley. Lower Ludlow, Church Hill Quarry, Leintwardine, Herefordshire. Reading University collection, E 299, Revultex cast ×2¼.

Figs. 2–5. *Cicerocrinus elegans* Sollas. Upper Ludlow. 2, BM E 26071a, ×2, Whitcliffe, Ludlow, Shropshire. 3, BM E 5726, ×4, wax squeeze of the holotype of *C. tenuis* (Jaekel); quarry by old bridge, Ludlow. Photo supplied by British Museum (Natural History). 4–5, holotype, OM c 80, fig. 4 ×1, fig. 5 ×2; unlocalized.

Figs. 6–7. *Mastigocrinus bravoniensis* sp. nov. Lower Ludlow, Leintwardine, Herefordshire. 6, paratype, OM c 84, Revultex cast, ×4. 7, holotype, GSM 89994, Revultex cast, ×6, posterior side of crown showing anal tube.

Figs. 8–9. *Gissocrinus ludensis* sp. nov. Lower Ludlow, Church Hill Quarry, Leintwardine, Herefordshire. 8, holotype, BM E 26573, Revultex cast, ×1½. 9, paratype, BM E 26577, external mould, ×1½.



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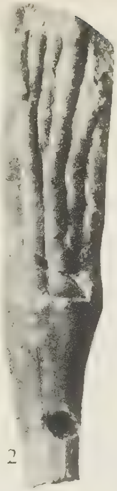

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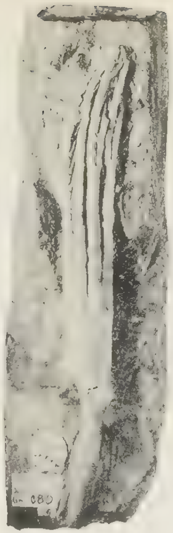

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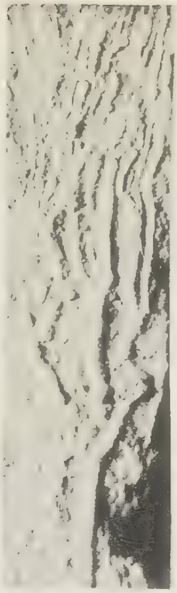

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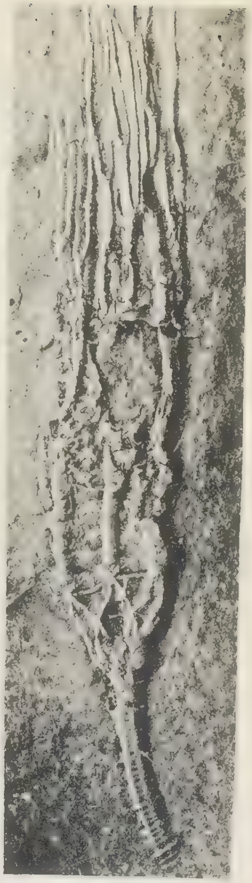

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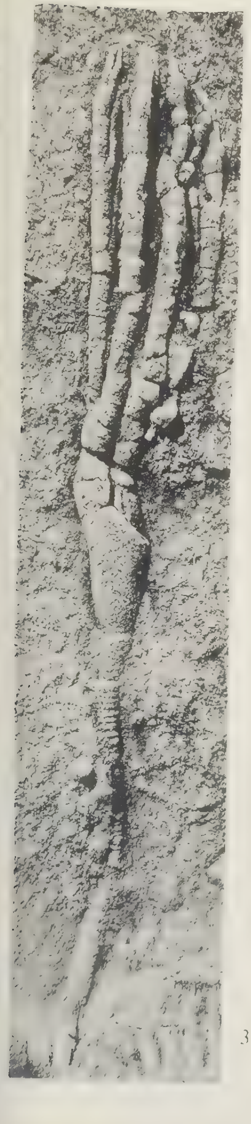

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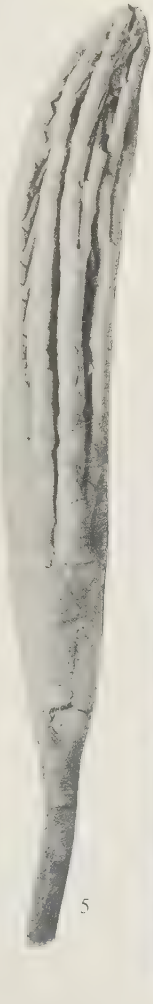

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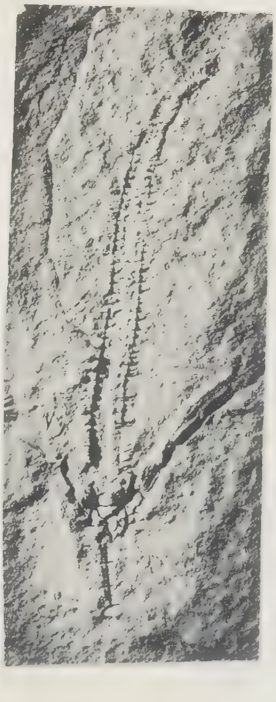

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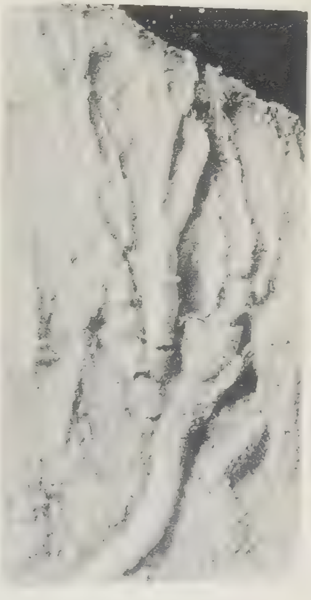

RAMSBOTTOM, Ludlovian crinoidea

a farm called 'Gumma', 1½ miles west of Presteigne. The old Geological Survey map, dated 1850, however, calls this farm 'Gomey'. There is doubt, moreover, as to which is 'Gomey Quarry', for locally no quarry is known by this name. There is an old, but still sporadically worked, quarry near the road ¼ mile north-east of Gumma Farm, now called Rock Bridge Quarry and this seems to be the most likely place from which the holotype of *C. anglicus* came. Collecting in this quarry by the writer yielded no specimens of *Cicerocrinus*, but this is not surprising when the rarity of this genus is considered.

With regard to the horizon, Dr. C. H. Holland, who is studying the stratigraphy of the Presteigne area, tells me that the whole of the rocks surrounding Gumma Farm for some distance, and including Rock Bridge Quarry, belong to the upper part of the Upper Ludlow, and not to the Lower Ludlow as was stated by Jaekel.

Genus PISOCRINUS de Koninck 1858

Type species by subsequent designation of S. A. Miller 1889: *Pisocrinus pilula* de Koninck, Wenlock Limestone, Dudley.

Diagnosis. A genus of Pisocrinidae in which the cup is well marked off from the stem, with unbranched non-pinnulate arms and with the radials bearing lateral processes. Basals five.

Pisocrinus cf. *sphericus* Rowley

Plate 21, fig. 1

A single almost complete specimen is figured here (Reading University collection E 299) from the Lower Ludlow (*Monograptus leintwardinensis* Zone) at Church Hill Quarry, Leintwardine. It was collected by Professor H. L. Hawkins during excavations in the quarry in 1926 (Hawkins and Hampton 1927). It has a small globular cup, a stem formed of columnals of equal length, and very short arms composed of only four brachials, the first of which is very short. The arms are possibly incomplete. The basals appear to be hidden by the stem, so that this specimen cannot belong to *P. pilula* de Koninck. It recalls *P. sphericus* Rowley from the Brownsport Formation of Tennessee, but in the absence of comparative material the determination must remain indefinite.

Sub-class CAMERATA Wachsmuth and Springer

Genus HAPALOCRINUS Jaekel 1895

Type species by monotypy: *H. elegans* Jaekel, Lower Devonian, Germany.

Diagnosis. A genus of Hapalocrinidae with two to four unbranched arms in each ray; brachials cuneate uniserial, each brachial bearing one pinnule, these coming off on each side alternately; interbrachials 1–2.

Hapalocrinus quinquepennis (Salter MS.) sp. nov.

Plate 20, figs. 1–3

Platycrinus quinquepennis Salter 1878, p. 116 (*nom. nud.*).
Crinoid sp.—La Touche 1884, pl. 17, fig. 550.

Holotype. BM E 26576*a*. *Paratypes*. BM E 14900, GSM 89897.

Occurrence. The specimens come from the Lower Ludlow Beds (*Monograptus leintwardinensis* Zone) at Leintwardine, Herefordshire. The British Museum specimens are from Church Hill Quarry, Leintwardine. Also known from the Lower Ludlow Beds at Ludlow (GSM 89905).

Diagnosis. A large species of *Hapalocrinus* with the surface of the cup plates smooth, the radial facets occupying about two-thirds of the width of the radials. Arms branch once only. Stem without cirri.

Description. A large species, a typical crown measuring about 60 mm. in height. Cup obpyriform, tubular above, about as wide as high. Basals about half the height of the radials, which are higher than wide, the radial facets occupying about two-thirds of the total width of the radials. The surface of the cup plates is smooth. Primibrachs two, with conspicuous brachial facets. Three or four secundibrachs without pinnules, followed by uniserial or slightly cuneate brachials. Arms branch once only, giving ten rami. Each brachial bears a pinnule, these being given off on each side alternately from the thicker ends of the brachials. Brachials short, nearly twice as wide as high. Interbrachial areas with one plate, followed by two smaller ones in the second row; none of these plates reaches far down into the cup. One interbrachial plate is sometimes a little larger than the others, and this is interpreted as being the posterior one. Tegmen not seen. Stem formed of alternating nodals and internodals, the nodals becoming less prominent and less numerous distally, and the length of the columnals increases distally. No trace of cirri are seen.

Discussion. All the available material of this species is represented by impressions, as is usual at Leintwardine, and the species has been studied with the aid of Revultex impressions. The large size of this species is the main distinguishing feature, since it is nearly twice as large as any of the other described species of *Hapalocrinus*. Salter (1878) labelled several specimens in the Geological Survey Museum as *Platycrinus quinquepennis*, but only the names appear in the published catalogue of 1878. La Touche figured a specimen which was formerly in the Ludlow Museum, but the figure is so generalized that the specimen has not been recognized among the specimens transferred from the Ludlow Museum to the British Museum (Natural History).

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SOME MESOZOIC ADHERENT FORAMINIFERA

by TOM BARNARD

ABSTRACT. The relationships between certain common Mesozoic species of adherent foraminifera are discussed. The wall structure appears to be the deciding factor in the correct placing of these genera. One new genus *Arenonina*, with type species *Arenonina cretacea* sp. nov., is proposed. An account of the evolution of the *Bullopora–Vitriwebbina* group is given. Most of the important species of Mesozoic adherent foraminifera are figured, although full synonymies are not considered desirable at this stage in our knowledge.

INTRODUCTION

SINCE Quenstedt (1856) gave the first description of an adherent foraminifer from the Lias, the subject has gradually become involved due to the introduction of new genera and species. In spite of an attempt by Macfadyen (1941) to clear up some of the problems, a number of recent papers has added to the confusion, so that further work on this group of foraminifera seemed necessary.

The present author has collected material from many levels in the Mesozoic, and found specimens adhering to crinoid ossicles and pinnules, fragments of shells of lamellibranchs, brachiopods, and echinoids. A few were also found adhering to inorganic fragments, mostly ooliths. In thin-sections of oolitic limestones from the Middle and Upper Jurassic many foraminifera were seen to be fixed to ooliths.

The author acknowledges a grant from the Central Research Fund of the University of London which partly defrayed the cost of collecting material.

Problems of nomenclature. The chief problems involved in a study of fossil adherent foraminifera are due to the inadvertent mixing of genera by some authors. This is perhaps due to the different states of preservation of the specimens. In most cases it is necessary to make extensive use of thin-sections to determine the wall structure. Authors often remark on the colour of specimens, giving the impression that milky-white tests are imperforate porcellaneous foraminifera. In many cases this is not true, however, and a grade in colour is found within one species, due to different states of preservation.

The initial ends of specimens are not often preserved and this too has led to confusion, especially where end-chambers are similar in shape.

In the present paper the chief 'genera' discussed are *Ammovertella*, *Bdelloidina*, *Bullopora*, *Nubeculinella*, *Placopsilina*, *Tolypammina*, *Vitriwebbina*, and *Webbina*.

DISCUSSION OF CERTAIN GENERA

(*a*) *Forms with agglutinated tests*

Genus TOLYPAMMINA Rhumbler 1895

Type species *Hyperammina vagans* Brady

Rhumbler (1895) separated the genus *Tolypammina* from *Hyperammina* on account of the adherent nature of the former, describing it as 'Gehäuse mehr oder weniger festgewachsen, mit kugliger oder ovaler Anfangskammer, sonst eine gleich weite Rohre dar-

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stellend, welche sich in unregelmäßigen Hin- und Herwindungen aufknäuelt'. The figure of the type *H. vagans* Brady, differs somewhat from the Mesozoic adherent forms in having a more tortuous shape.

A study of the type specimen preserved in the Brady Collection, British Museum (Natural History), together with material from the Challenger and Porcupine Collections, reveals that the specimens differ appreciably from the description given by Cushman (1940, p. 95), and assumed to be correct by many workers.

Brady's specimens show no sign of an initial coiled portion, but consist of a globular proloculum, followed by an irregularly winding tube. Many forms described as *Tolypammina* have an initial coiled portion, for example *Tolypammina delicatula* Cushman and Waters (1928, p. 62, pl. 8, fig. 3), and these forms should be transferred to *Ammovertella*. Cushman (1940, p. 92) gives a copy of Brady's type figure in a 'phylogenetic' chart of the family Ammodiscidae. Hence it is apparent that Cushman places forms with or without initial coils in the same genus.

Examples of *Tolypammina* are figured on Pl. 22, figs. 3, 4; Pl. 23, fig. 1*b*.

Genus AMMOVERTELLA Cushman 1927

Type species *Ammodiscus* (*Psammophis*) *inversus* Schellwien 1898

Cushman (1927) selected *Psammophis inversus* Schellwien as the genotype for a new genus *Ammovertella*, which had previously been considered as *Psammophis*, a sub-genus of *Ammodiscus*. The form is adherent, with a planispiral initial portion, followed by an irregularly unwinding tube. The aperture is the open end of this tube. Many forms from the Mesozoic are similar to the type figure, even to the extent of having a reverse direction of coiling, a character often seen in the free foraminifera *Ammodiscus*.

In both *Tolypammina* and *Ammovertella* the final tubular portion of the test is similar, and without a study of the initial part, it is impossible to separate the genera. *Ammovertella liassica* Barnard is figured on Pl. 22, figs. 5, 6.

Genus PLACOPSILINA d'Orbigny 1850

Type species *Placopsilina cenomana* d'Orbigny

Placopsilina differs from the two genera discussed above in that it is a polythalmous form with distinct chambers. D'Orbigny (1850, p. 259) states 'Ce genre ressemble aux *Truncatulina*, mais est toujours fixe . . .'.

Originally the species was not figured by d'Orbigny, and Cushman (1920) designated *Placopsina cenomana* d'Orbigny as the type species. Cushman (1940) figures *Pl. cenomana* (after Reuss), showing a spiral initial portion, and states (p. 191) '. . . early portion close coiled, later portions uncoiled and spreading out in a generally linear series . . .'.

Many specimens of adherent vitreous foraminifera having hemispherical chambers secrete a lower boundary wall to each chamber. This rests on and adheres to the surface on which the foraminifer grows. When tests are crushed into this lower surface a pseudo-arenaceous wall is produced, and specimens belonging to *Bullopora*, *Webbina*, and *Vitriwebbina* have been included in *Placopsilina*.

Two different forms, however, do exist, one having an initial coiled stage followed by an uncoiled portion, which varies appreciably in length, and the other having no initial coil. In the former the chambers in later stages of the test abut directly against one another, with no well-marked constriction along the septa, whereas in the latter the chambers tend to be hemispherical, with constricted necks connecting them. Most forms which have been described as having an initial coil are confined to the Cretaceous. *Placopsilina expansa* Tappan (1943), *Pl. longa* Tappan (1940, 1943), and *Pl. minima* Tappan (1943) are three examples from the Lower Cretaceous of America, in which the uncoiled portion of the test is of varying length.

Many specimens from the Lias and Oolites described by Terquem as belonging to the genus *Placopsilina* were on examination found to be crushed specimens of *Bullopora rostrata* Quenstedt and *B. globulata* Barnard.

The problem arises as to what d'Orbigny's original specimens looked like. Both Reuss and Chapman figure *Pl. cenomana* d'Orbigny as having a well-marked initial coil, and if these figures are a correct interpretation of d'Orbigny's specimen, then the material from the Jurassic, having hemispherical chambers, should be assigned to a different genus. However, the present author thinks that it is undesirable to take this step until more evidence is available.

Species of *Placopsilina* are figured on Pl. 23, fig. 2, and Pl. 25, fig. 4.

Genus BDELLOIDINA Carter 1877

Type species *Bdelloidina aggregata* Carter 1877

In a recent paper Loeblich and Tappan (1955, p. 21) state that 'Carter's specimens have not been found but were from excavations on the surface of a mass of *Siderasteraea*, exact locality not given'. These authors (1955, pl. 3, figs. 9, 10) show adherent foraminifera with internal structures in the forms of interior secondary septa crossing the chambers vertically, with numerous internal pores. These characters are of sufficient generic importance to separate this genus from the specimens from the Upper Cretaceous (Chalk) of England, which otherwise have a superficial external resemblance to *Bdelloidina*, and could be confused with it. They are described below as a new genus.

Genus ARENONINA gen. nov.

Type species *Arenonina cretacea* sp. nov.

Diagnosis. Test attached, wall arenaceous, composed of fine particles in a calcareous cement. The test consists of an initial spire followed by a uniserial arrangement of the chambers. The spire consists of four to eight chambers in each whorl, and usually of less than two whorls. In the spire the chambers are triangular in plan view, and swollen so that the periphery is lobulate. Near the periphery the sutures are deep and the chambers constricted, but become shallow and indistinct towards the central umbilicus.

Although the height of the chambers increases slowly, the distance from the periphery to the umbilicus may increase rapidly, so that after the initial spire the chambers may overlap one another on to the earlier portion of the test. Sometimes the test tends to become loosely coiled before passing into the uniserial portion. Within the uniserial part of the test the chambers are arcuate with parallel septa, little or no increase in height, but a rapid increase in length; so that the test becomes fan-shaped.

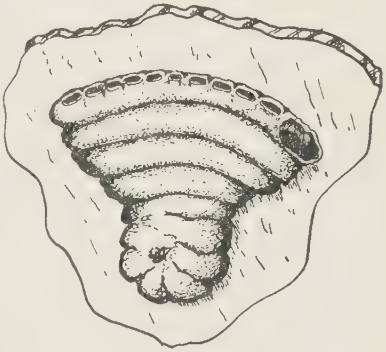
The aperture consists of a row of well-defined pores occurring along the full length of the apertural face. Each pore has a well-marked lip. The pores increase in size towards the edge of the test.

Arenonina cretacea sp. nov.

Plate 22, figs. 1 and 2; text-fig. 1

Description. Test adherent, arenaceous wall, with much calcareous cement. The test consists of an initial loose spire, followed by a uniserial series of chambers. The spire consists of four to eight chambers, with constricted sutures. These constrictions are deep at the outer margin of the test, but tend to become shallow and indistinct towards the umbilicus. The outer margin of the test is lobulate. The initial spire is followed by two to four chambers only slightly increasing in length, forming a short arcuate portion to the test. Finally the chambers increase rapidly in length until a fan-shaped test is formed.

In the early stages of the test the aperture appears to be a longitudinal slit running the full length of the apertural face. The specimens which show this may, however, be damaged. In forms having fan-shaped later chambers the aperture consists of a single row of pores, each pore surrounded by a distinct smooth lip. The pores increase in size from the centre of the test towards the periphery. Each pore occurs at the top of a small crenulation of the apertural face.



TEXT-FIG. 1. *Arenonina cretacea* gen. et sp. nov.

Holotype. British Museum (Natural History) P. 43656. Upper Chalk, Zone of *Micraster coranguinum*, Northfleet, Kent.

Range of specimens studied. Upper Chalk, Zones of *M. coranguinum* and *Belemnitella mucronata.*

(*b*) *Forms with calcareous tests*

Genus NUBECULINELLA Cushman 1930

Type species *Nubeculinella bigoti* Cushman

Cushman (1929, p. 134) selected *N. bigoti* as the genotype of *Nubeculinella*, this form coming from the Oxfordian of Auberville. Macfadyen (1941) considered that *Nubeculinella* to be a synonym of *Bullopora* Quenstedt. Most of the forms described were in fact collected from the Oxford Clay of Warboys, Huntingdonshire, and were identical with *N. bigoti* Cushman.

Sections through the walls of similar fossils show an imperforate porcellaneous wall structure, with no radially arranged calcite visible, even when highly magnified. The test has an initial globular proloculum around which the second chamber is planispirally wound. This initial part of the test is followed by a linear series of hemielliptical or elongated chambers.

Cushman's figures show the specimens to have holes on the top of the dome-shaped chambers. This is often seen in fossil forms where the wall has been partially removed. If the chambers are filled with secondary calcite and the wall removed, the form appears to have a vitreous, hyaline wall and consequently has often been assigned to *Bullopora*.

In some specimens, however, the replacement is partial, and part of the wall remains, serving as a means towards identifying the species.

After the initial spire the general shape of the chambers resembles those in *Bullopora* and further confusion exists. Two species of *Nubeculinella* are figured on Pl. 23, figs. 1*a*, 3, and Pl. 25, fig. 5.

Genus WEBBINA d'Orbigny 1839

Type species *Webbina rugosa* d'Orbigny 1839

Although d'Orbigny originally figured and described the genus (1839) a type was not designated. Loeblich and Tappan (1955, p. 23) point out that *Webbina rugosa* d'Orbigny, a Recent form, was subsequently designated by d'Orbigny in Barker-Webb and Berthelot (1839, p. 126); it was the first species published under that genus. Three authors, Galloway (1933, p. 296), Cushman (1940, p. 303), and Loeblich and Tappan (1955, p. 23) all disagree regarding the wall structure. The latter, however, state that 'the original figures given by d'Orbigny for this species are very misleading. The holotype does not appear either coarsely perforate or with a roughened surface except for the fimbriate-appearing keel.'

The question of wall structure of this form is important when considered in relation to the genera *Bullopora* and *Vitriwebbina*. Sollas (1877, p. 103) describes sections of two species, *W. laevis* and *W. tuberculata*, both from the Cambridge Greensand (Albian). These forms have radial calcite forming the wall, and are said to be perforate.

Most forms assigned to either the genus *Bullopora* or *Vitriwebbina* have a thin base to each chamber, sometimes this protrudes beyond the sides of the chambers, it may be that this character which is said to be diagnostic of *Webbina* is common to all three 'genera'.

It seems probable that the species proposed by Sollas (1877) belong to the genus *Vitriwebbina* as stated by Chapman (1892), and these forms may not be the same genus as the Recent species *W. rugosa* d'Orbigny.

Genus VITRIWEBBINA Chapman 1892

Type species *Vitriwebbina sollasi* Chapman

Chapman 1892 created the new genus *Vitriwebbina* and included part of both d'Orbigny's and Sollas's *Webbina*. Cushman (1927) designated *V. sollasi* Chapman 1892 as the type species, but later, however (1940), decided that *Vitriwebbina* was a synonym of *Bullopora*.

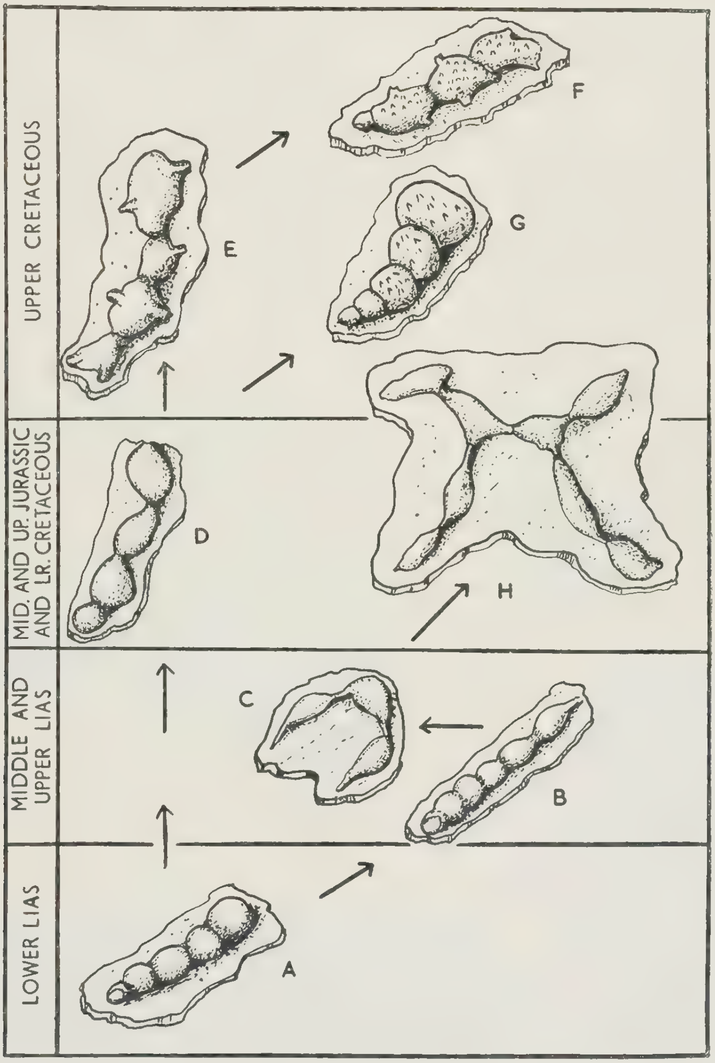
Genus BULLOPORA Quenstedt 1856

Type species *Bullopora rostrata* Quenstedt

The taxonomy of the calcareous adherent foraminifera depends on the wall structure of the genera *Webbina*, *Vitriwebbina*, and *Bullopora*, whether these forms have radial calcite forming the walls, and whether they are synonymous.

Although *Bullopora rostrata* Quenstedt was the first species to be named by Quenstedt, another form was first figured and described, but left unnamed. No type was designated and so *B. rostrata* has become the type. Quenstedt's figures, although indistinct, show the two forms to have strong differences. *Bullopora sp.* (the first described species) Quenstedt (p. 292, pl. 41, fig. 26) does not show the long tubular necks so characteristic and well marked in *B. rostrata* Quenstedt (p. 554, pl. 73, fig. 28). This fundamental difference between the two forms has been remarked on before, and the *Bullopora sp.* of Quenstedt would fall within the present author's conception of his species *Bullopora globulata* Barnard (1950*a*).

Bullopora has been referred to several different families of foraminifera. Macfadyan (1941) places it in the Ophthalminiidae, but suggests *Bullopora* is synonymous with *Nubeculinella*, an imperforate porcellaneous form. Cushman (1940) and Tappan (1943) place it in the Polymorphinidae. The present author considers *Bullopora* and *Vitriwebbina* synonymous, and that both belong to the vitreous, hyaline foraminifera. The initial part of the test consists of a hemispherical proloculum followed by a chamber which partly surrounds this, a character often seen in the non-adherent foraminifera belonging to the



TEXT-FIG. 2. Outline of evolution of *Bullopora*.

family Lagenidae. Thus the present author assigns the genus *Bullopora* to the family Lagenidae, with the possibility in mind that *Bullopora* may prove a synonym of *Webbina*, when more is known about the type specimen of the latter.

Examples of *Bullopora* are figured on Pl. 24 and 25.

Evolution of Bullopora. If *Vitriwebbina* and *Bullopora* are synonymous, then an account of their evolution throughout the Mesozoic can be given (text-fig. 2).

EXPLANATION OF PLATE 22

All illustrations are unretouched photographs and all are magnified ×30 except fig. 6 which is ×60. Unless otherwise stated the specimens are in the author's collection.

Figs. 1–2. *Arenonina cretacea* gen. et sp. nov. 1, Holotype, Upper Cretaceous, Zone of *Micraster coranguinum*, Northfleet, Kent. British Museum (Nat. Hist.) P. 43656. 2, Paratype, Upper Cretaceous, Zone of *Belemnitella mucronata*, Paulsgrove, Norfolk.

Figs. 3–4. *Tolypammina flagellum* (Terquem). 3, Upper Lias, Zone of *Dactylioceras tenuicostatum*, Byfield, Northamptonshire. 4, Lower Lias, Zone of *Scamnoceras angulatum*, Lyme Regis, Dorset.

Figs. 5–6. *Ammovertella liassica* Barnard. 5, Fuller's Earth, Bathonian, Langton Herring, Dorset. 6, Upper Lias, Zone of *Dactylioceras tenuicostatum*, Byfield, Northamptonshire.

EXPLANATION OF PLATE 23

All illustrations are unretouched photographs. The specimens are in the author's collection.

Fig. 1. (*a*) *Nubeculinella bigoti* Cushman, ×30. (*b*) *Tolypammina flagellum* (Terquem), ×30. Upper Oxford Clay, Zone of *Cardioceras praecordatum*, Warboys, Huntingdonshire.

Fig. 2. *Placopsilina sp.*, ×60. Lower Lias, Zone of *Scamnoceras angulatum*, Lyme Regis, Dorset.

Fig. 3. *Nubeculinella filiformis* Paalzow, ×45. Upper Lias, Zone of *Dactylioceras tenuicostatum*, Byfield, Northamptonshire.

EXPLANATION OF PLATE 24

All illustrations are unretouched photographs and all are magnified ×30. All specimens except where otherwise stated are in the author's collection.

Fig. 1. *Bullopora sollasi* var. *gonoidea* (Chapman). Holotype, Gault Clay, Copt Point, Folkestone, Kent. British Museum (Nat. Hist.) P. 5249.

Fig. 2. *Bullopora sollasi* (Chapman). Holotype, Gault Clay, Copt Point, Folkestone, Kent. British Museum (Nat. Hist.) P. 4719.

Fig. 3. *Bullopora* cf. *globulata* Barnard. Upper Cretaceous, Zone of *Belemnitella mucronata*, New Catton, Norwich, Norfolk.

Fig. 4. *Bullopora rostrata* Quenstedt. Upper Oxford Clay, Zone of *Cardiocera praecordatum*, Warboys, Huntingdonshire.

Fig. 5. *Bullopora globulata* Barnard. Lower Lias, Zone of *Scamnoceras angulatum*, Lyme Regis, Dorset.

Fig. 6. *Bullopora rugosa* d'Orbigny. Cenomanian, Barrington, Cambridgeshire.

EXPLANATION OF PLATE 25

All illustrations are unretouched photographs and all are magnified ×30 except fig. 2 which is ×10. All specimens except where otherwise stated are in the author's collection.

Fig. 1. *Bullopora sollasi* var. *gonoidea* (Chapman). Upper Cretaceous, Taylor Formation, Texas.

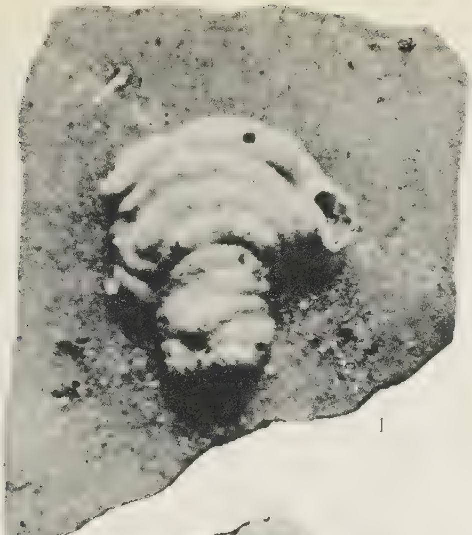
Fig. 2. ? *Neoflabellina* cf. *angulosa* (d'Orbigny). Upper Chalk, Zone of *Belemnitella mucronata*, Tharston, Norfolk.

Fig. 3. *Bullopora* cf. *globulata* Barnard. Upper Cretaceous, Zone of *Belemnitella mucronata*, New Catton, Norwich, Norfolk.

Fig. 4. *Placopsilina cenomana* d'Orbigny. Cenomanian, Barrington, Cambridgeshire.

Fig. 5. (*a*) *Nubeculinella bigoti* Cushman. (*b*) *Bullopora rostrata* Quenstedt. Upper Oxford Clay, Zone of *Cardioceras praecordatum*, Warboys, Huntingdonshire.

Figs. 6–7. *Bullopora* cf. *rostrata* Quenstedt. Upper Cretaceous, Taylor Formation, Texas.



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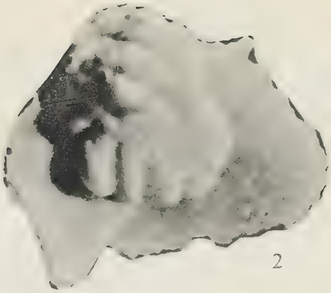

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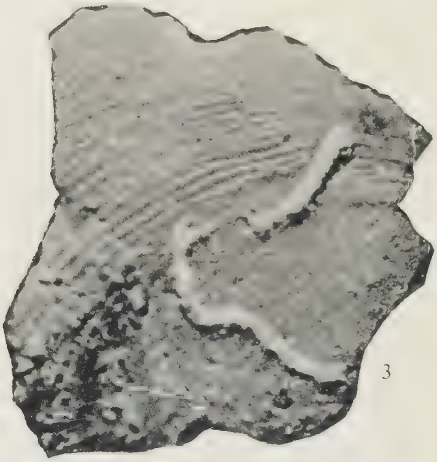

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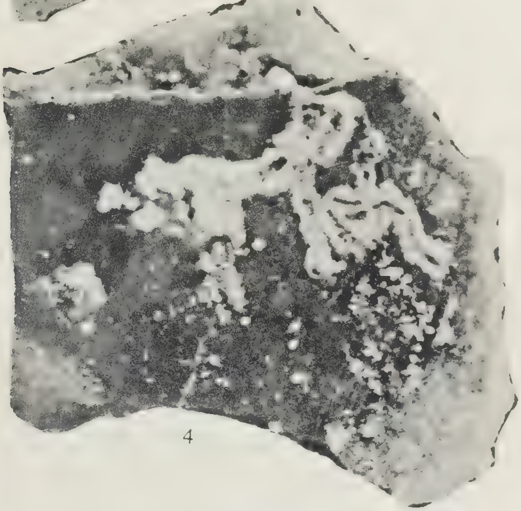

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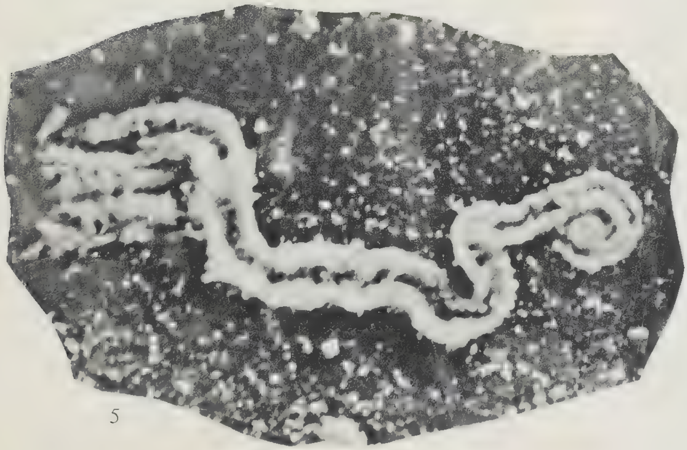

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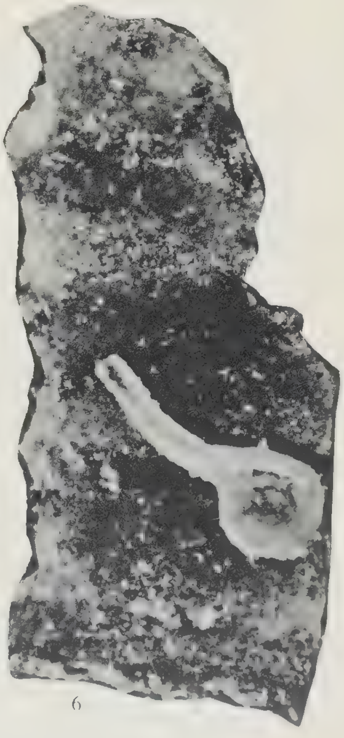
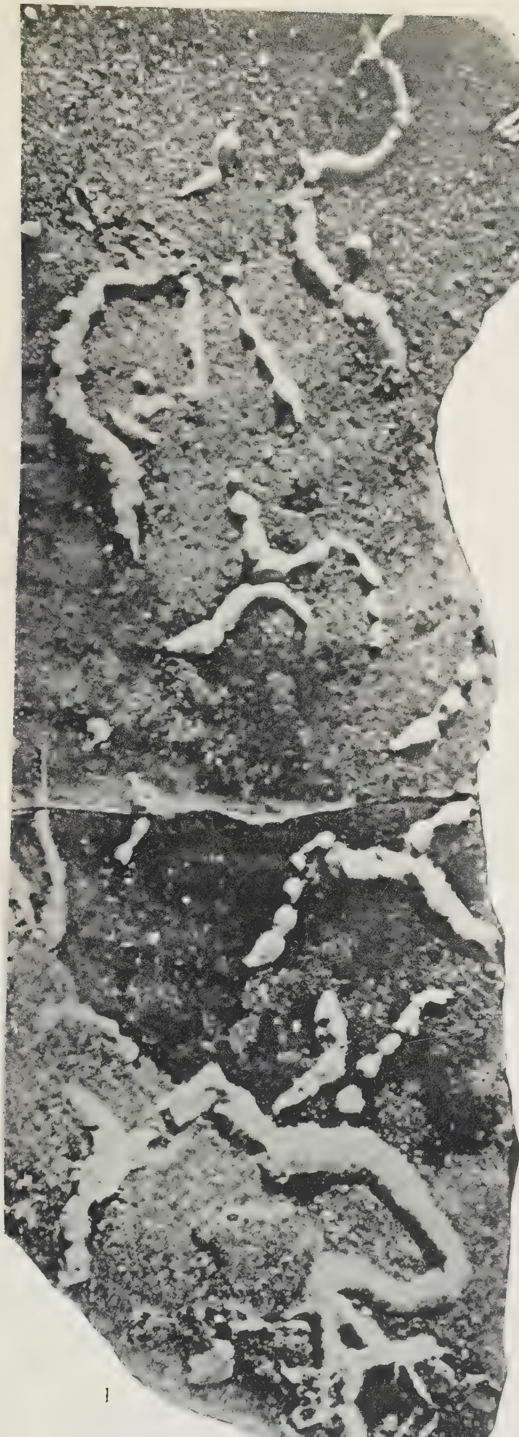


6

BARNARD, Mesozoic adherent foraminifera

PLATE 23



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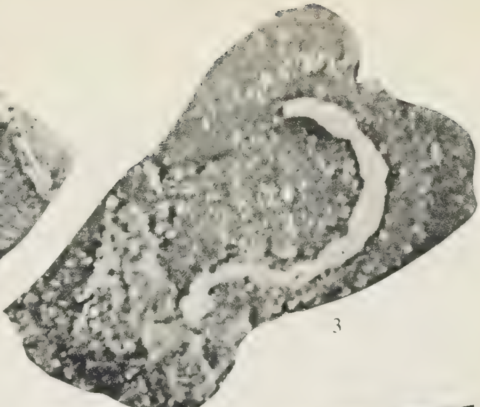

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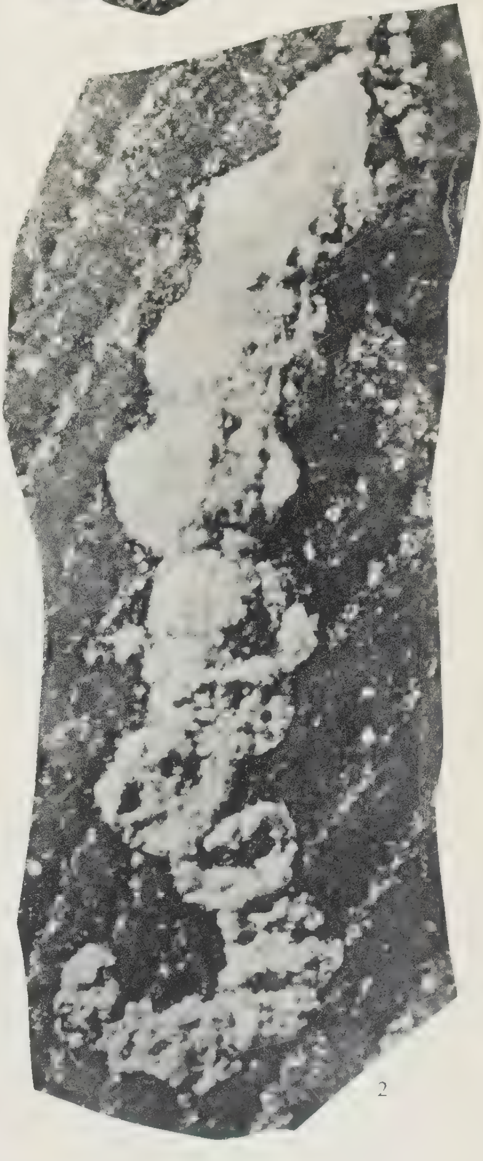

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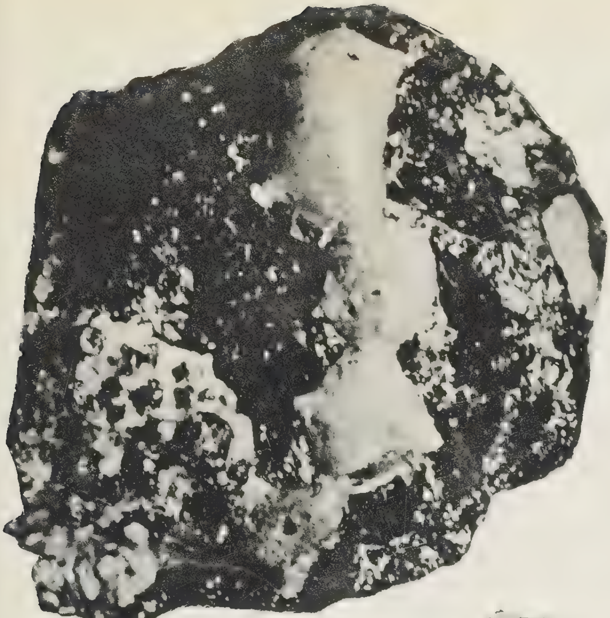

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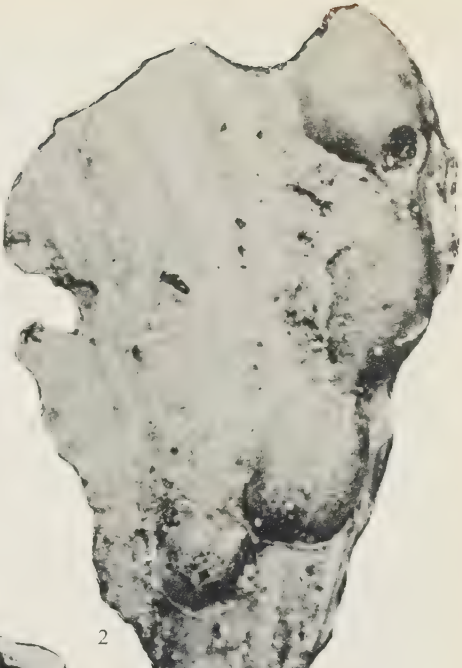

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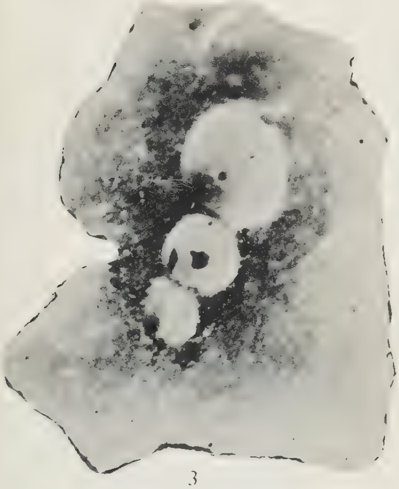

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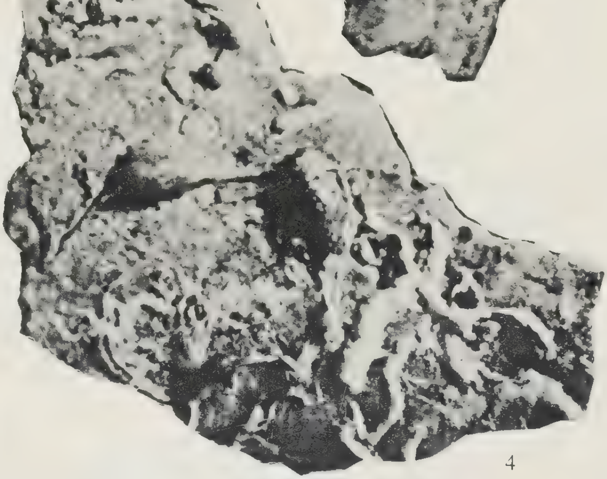

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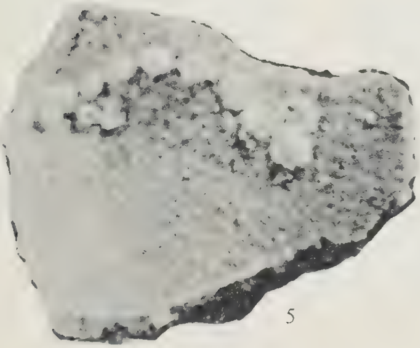

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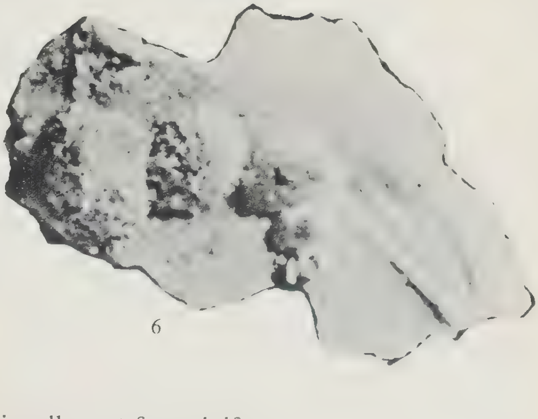

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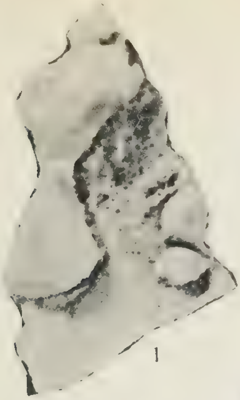
BARNARD, Mesozoic adherent foraminifera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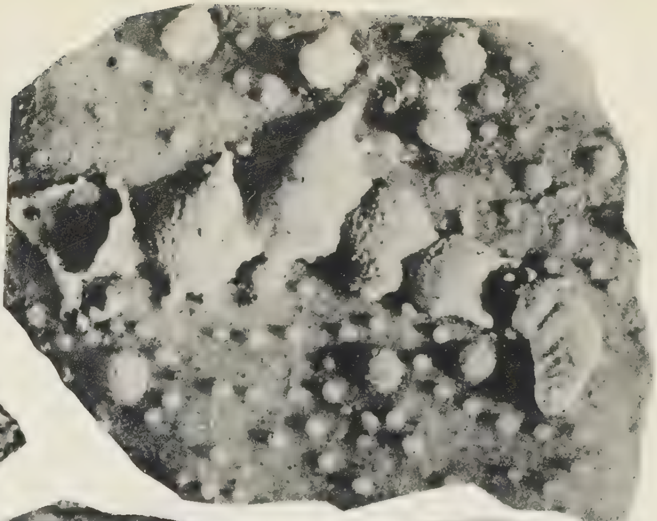
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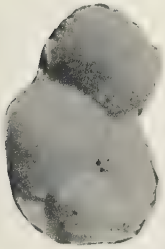
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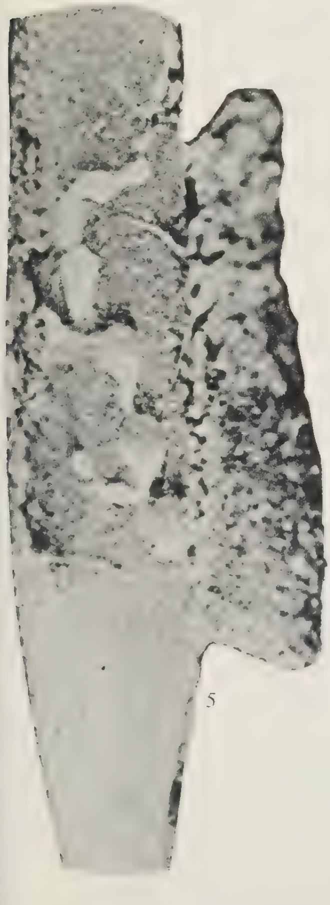
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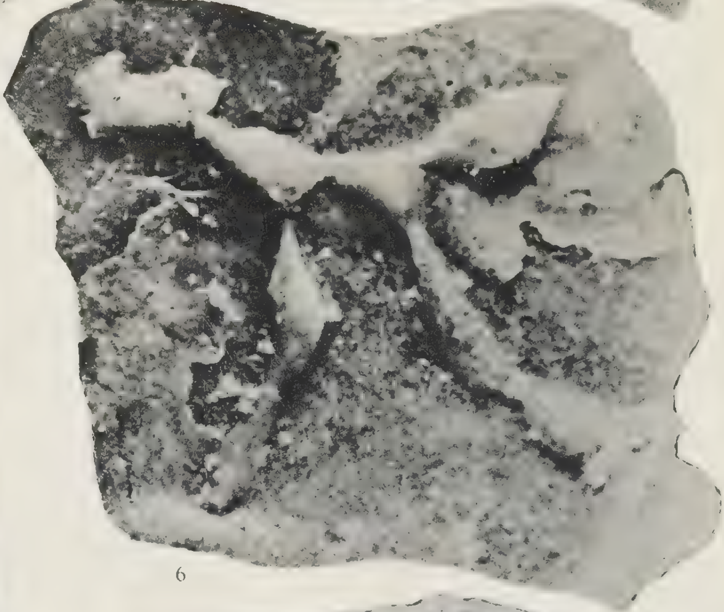
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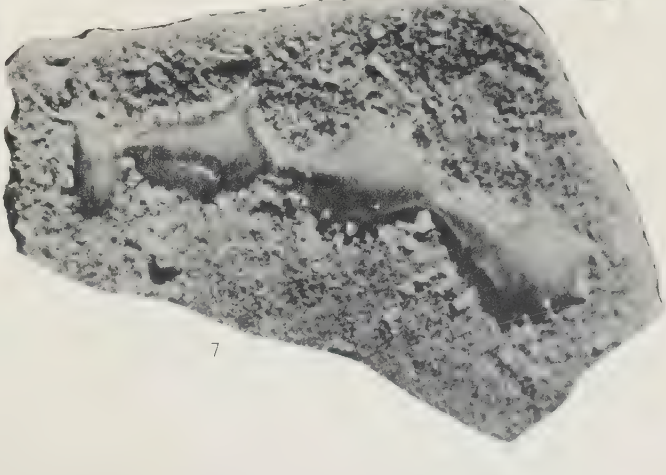
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BARNARD, Mesozoic adherent foraminifera

Form A shows a normal specimen of *Bullopora globulata* Barnard, which occurs in the Lower Lias and continues almost unchanged to the Cretaceous, where it has been called *Vitriwebbina laevis* (Sollas) by most authors.

In many Lagenids there is a tendency for later chambers to become elongate and constrictions to occur between the chambers. This is seen in Form B, occurring in the Middle and Upper Lias, *Bullopora rostrata* Quenstedt and *B. globulata* Barnard could be linked through this form. When the elongate constricted chambers occur after the second chamber, the Form C, *Bullopora rostrata* Quenstedt is developed. This form ranges from Middle Lias to Cretaceous, where it may show a tendency to branch, as in Form H. All these forms A, B, C, D, H have unornamented chambers with smooth peripheries.

Later in the Cretaceous two further trends develop. Form E shows a tendency for some of the chambers to develop small tubular extensions, which often become extended and fix on to small objects or irregularities on the host body, for instance the granules on echinoids.

Independently of this a further trend may be developed as in Forms F and G which have a hispid or rugose ornament. In some specimens early chambers are smooth and later ones are ornamented. This feature can occur in both forms, those with smooth peripheries and those with tubular extensions to the chambers.

The author (1949, p. 284) drew attention to a group of specimens showing a passage from a free unornamented *Neoflabellina* to an adherent hispid *Bullopora*. The question arises how this peculiar group, with what appears to be two distinctly different generic forms mixed in one specimen, could have arisen.

For a long time a similar, but less pronounced, problem has presented itself to the author in his studies of other members of the Lagenidae, particularly short-ranged forms which appear to be made up of two generic forms. The suggestion is put forward that these forms may have arisen as hybrids from interbreeding between two genera.

As far as the author has been able to ascertain, the form on Pl. 25, fig. 2 is the only one described which changes not only its growth pattern, but also its mode of life, from a free to a fixed species.

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THE MICROSPORE GENUS *SIMOZONOTRILETES*

by H. J. SULLIVAN

ABSTRACT. The microspore genus *Simozonotriletes* is reinterpreted in the light of new material obtained from three horizons in the Westphalian sequence of Great Britain. The spores are assigned to nine varieties of the type species *Simozonotriletes intortus* (Waltz). The species *S. sublobatus* (Waltz) is reduced to varietal status; *Triquitrites trivalvis* (Waltz) is transferred to *Simozonotriletes* and also recognized as an infraspecific category. The variation in the spore assemblages is described and the stratigraphical occurrences noted.

INTRODUCTION

THIS account deals with the morphological variation exhibited by a group of triangular zonate microspores which have been obtained from a cannel coal at the top of the Middle Fenton Seam and its overlying non-marine shale at the Coldbath opencast site, near Barnsley, Yorkshire (Floral Zone Upper Westphalian A). These spores formed only a small proportion of the total assemblage from any one microscope separation and, in the sense of Raistrick, would be termed 'accessory'. However, in the course of examining a large number of slides over 100 specimens have been recognized, and these have been used to illustrate the present study. Other examples from the cannel coal, Hazelwood opencast site, Coed Talon, Flintshire (Floral Zone Middle Westphalian A); and a cannel coal in the Barnsley Seam, Firbeck Colliery, near Worksop, Nottinghamshire (Floral Zone Middle Westphalian B), have been included in this paper to supplement the evidence provided by the Fenton assemblages.

The spores showed a considerable amount of variation principally in the structure of the exine external to the central area, and in the shape of the grain in proximo-distal orientation. A number of the examples could readily be referred to *Simozonotriletes* Potonié and Kremp, but in addition there were allied forms which possessed characters hitherto undescribed in this genus. Many diverse types were represented, but were all related in that the entire collection displayed continuous morphological variation along certain well-defined trends. The end members of these trends were of widely dissimilar aspect, and on the basis of the existing classifications, the differences could be interpreted as sufficient to warrant generic status. However, since there were no demonstrable discontinuities in the variational pattern all the forms are here considered as constituting one species; any subdivision should therefore be limited to the infraspecific level.

While a trinomial nomenclature may appear cumbersome to the stratigraphical palynologist, whose prime concern is the application of spores to the practical problems of zoning and correlation, it is nevertheless amply justified in that it gives a more precise expression of morphological relationship and possibly also of botanical affinity.

Due regard has been paid to the range and pattern of variation in the erection of taxonomic units. In the analysis of a small number of specimens undue emphasis may be given to individual variants because of the incomplete representation of their relationhips. This applies particularly in the present instance when we are dealing with one of the rarer types of spores. If a restricted number of spores had been considered, divorced from the picture of continuous variation which emerges when the total population is

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studied, the apparent differences they displayed would have suggested the existence of several species or even genera. The nomenclatural treatment would then have borne no relation to their natural alliance. The evidence is not conclusive to show whether or not these spores were derived from the same species of parent plant, but the close and intergrated morphological similarities they display may well suggest a common origin.

The range and pattern of variation of the spores in the shale were comparable in almost every respect to those in the underlying cannel coal, and the assemblages are treated as one in the description of the morphology. The morphological terms used in the designation of the taxonomic units are those defined by Potonié and Kremp (1955, pp. 9–15).

The spores were isolated by macerating a crushed sample of coal with Schulze solution followed by washing with 10 per cent. caustic potash and distilled water. Preliminary treatment with warm hydrofluoric acid was necessary in the case of the shale to remove the mineral matter. Permanent mounts of the microscope separations were made in glycerine jelly and all the slides are now housed in the collection of the Micropalaeontological section of the Geology Department, Sheffield University.

The author is deeply indebted to Professor L. R. Moore for his constant help and guidance throughout all stages of the work, and to Mr. P. C. Sylvester-Bradley for much useful discussion and advice. Mr. R. Neves has read the manuscript and offered a number of suggestions. Thanks are also due to Mr. G. S. Bryant for his help in the production of the plates, and to Miss P. Linnett for her assistance in drawing the text-figures.

The contents of this paper form part of an investigation into the microfloral remains of cannel coals and associated carbonaceous sediments. The work is being carried out at the Geology Department, University of Sheffield, under a tenure of a Town Trustees Fellowship and a State supplemental award.

SYSTEMATIC REVISION

The name *Simozonotriletes* was introduced by Naumova (1937, p. 355) for a 'subgroup' of microspores included in *Zonotriletes* Waltz 1935. The 'subgroup' is now considered equivalent to a taxon of generic rank. Naumova gave only a brief diagnosis and named no species. Three species of spores *Zonotriletes intortus*, *Z. sublobatus*, and *Z. auritus*, described by Waltz in Luber and Waltz (1938), were subsequently transferred to *Simozonotriletes* by Potonié and Kremp (1954, p. 159; 1956*a*, pp. 109–10). They gave a more complete account of the generic characters and selected *S. intortus* as the type species.

When the genus *Simozonotriletes*, as herein interpreted, is placed within the framework of the classification proposed by Potonié and Kremp (1954), certain inconsistencies arise. It is hoped to discuss the question of its systematic position in a later paper, but a revision of the diagnostic characters used in the definition of the suprageneric taxa of the subdivision Zonales would seem to be indicated.

Genus SIMOZONOTRILETES Potonié and Kremp, 1954

Type species *Simozonotriletes intortus* (Waltz) Potonié and Kremp 1954

Diagnosis. Trilete isospores or microspores; triangular in equatorial plane with convex to markedly concave sides and rounded apices; central area triangular, margin well defined and runs approximately parallel to the equator of the spore; exine levigate to infrapunctate or infragranulate; trilete rays exceed $\frac{2}{3}$ radius of central area; cingulum may be of uniform width and thickness but is frequently wider and thicker at the apices; it can also be differentiated into an outer dark zone and inner light zone; dark zone often expanded and thickened into smooth, pad-like valvae at the apices, and may be absent or discontinuous along the sides; in some forms thickened areas are also present in interradial regions; secondary folds absent due to good proximo-distal orientation; extrema lineamenta smooth to sinuous, sometimes incised.

Comparison and remarks. This genus resembles *Triquitrites* Wilson and Coe 1940, but may be distinguished from it by the presence of a well-defined central area. The auriculae in *Tripartites* Schemel 1950 are usually larger and show a tendency to frilling and fluting. *Anulatisporites* Potonié and Kremp 1954 has a more circular outline and the cingulum decreases in thickness towards the equator. Two species of *Simozonotriletes* are now recognized, viz. *S. intortus* and *S. auritus*. These can be differentiated on the basis of the trilete suture. The rays in *S. auritus* possess broad, prominent lips, whereas in *S. intortus* the lips are thin.

Simozonotriletes intortus (Waltz) Potonié and Kremp 1954

Diagnosis. Size 35–110 μ, trilete rays extend almost to the margin of the central area, lips thin, intratectum narrow; remainder as for genus.

Simozonotriletes intortus var. *intortus* (Waltz)

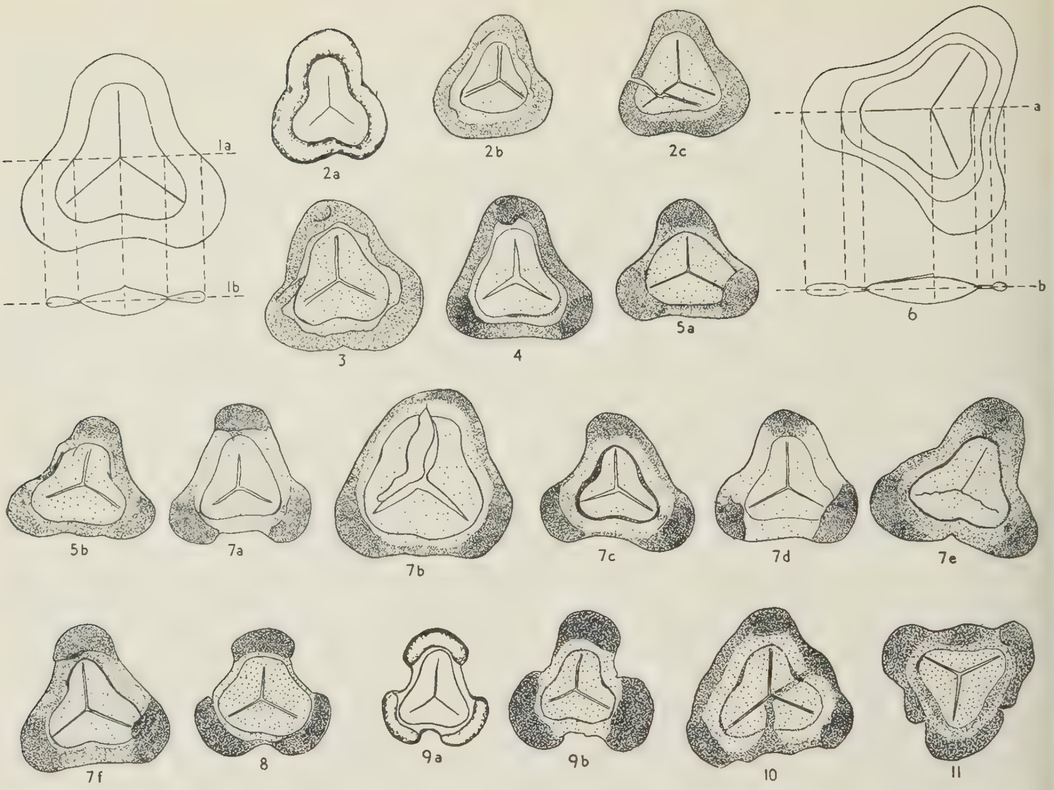
Plate 26, figs. 1–4; text-figs. 1, 2*a*–*c*

Zonotriletes intortus Waltz *in* Luber and Waltz 1938, pl. 2, fig. 24.
Simozonotriletes intortus (Waltz), Potonié and Kremp 1954, p. 189.
Simozonotriletes intortus (Waltz), Horst 1955, p. 183, pl. 22, figs. 52–54.

Holotype. Plate 2, fig. 24 of Luber and Waltz (1938), Moscow Brown Coal (reproduced as text-fig. 2*a*). *Figured material*. Slides M2C1d (152831), M2E7a (168719), M2C1c (295786), Middle Fenton coal and shale, near Barnsley, Yorkshire. Slide M9A3 (355654), Barnsley Seam, near Worksop, Nottinghamshire. Slide 17A1f (182710), Flint Cannel Coal, near Wrexham, Flintshire. All slides are in the collection of the Geology Department, University of Sheffield.

Diagnosis. Size 35–110 μ, holotype (measured from figure) approximately 60 μ; cingulum homogeneous or may show a division into dark and light zones; dark zone, if present, maintains a uniform width and thickness around the equator; cingulum not expanded and thickened at the apices.

Description. Colour yellow to brown. Triangular in equatorial outline with slightly concave or convex sides and rounded apices. The exine of the central area is levigate to infragranulate and often shows evidence of corrosion and decay. Trilete rays long and straight, extend almost to margin of central area. Some of the forms (e.g. text-fig. 2*a*; Pl. 26, fig. 1) possess an undifferentiated cingulum which is rounded at the equator (text-fig. 1), but in others (Pl. 26, fig. 4; text-fig. 2*b*) dark and light zones are present. In the spore figured on Pl. 26, fig. 3 the cingulum tends to be wider in the interradial regions where it overlaps on to the central area.



TEXT-FIGS. 1–11. *Simozonotriletes intortus* (Waltz).

Figs. 1, 2, var. *intortus* (Waltz). 1*a*, *b*, diagrammatic representation of polar view and hypothetical meridianal section, with undifferentiated cingulum. 2*a*, holotype redrawn from Luber and Waltz (1938), ×275. 2*b*, slide M2E7a ref. 168719 (see Pl. 26, fig. 2), Fenton shale, ×250. 2*c*, slide M17A1f ref. 182710, Flint Cannel Coal, ×250.

Fig. 3, var. *fentonensis* nov., holotype, ×250.

Fig. 4, var. *lineatus* nov., holotype, ×250.

Fig. 5, var. *sublobatus* (Waltz), ×250. 5*a*, slide M1B5 ref. 358698 (see Pl. 26, fig. 11), Fenton Cannel Coal. 5*b*, slide M2E4 ref. 169767, Fenton shale.

Figs. 6, 7, var. *polymorphosus* nov. 6*a*, *b*, diagrammatic representation of polar and hypothetical meridianal section. 7*a*, holotype. 7*b*, slide M2C1e ref. 208695. 7*c*, slide M2E7 ref. 101845. 7*d*, slide M2E7a ref. 237769. 7*e*, slide M1B5 ref. 338647. 7*f*, slide M1B4 ref. 210763 (see Pl. 27, fig. 11). 7*a*, *c*, *d* from Fenton shale, ×250; 7*b*, *e*, *f* from Fenton Cannel Coal, ×250.

Fig. 8, var. *concavus* nov., holotype, ×250.

Fig. 9, var. *trivalvis* (Waltz), ×250. 9*a*, holotype, redrawn from Luber and Waltz 1938. 9*b*, slide M2E7b ref. 460653 (see Pl. 28, fig. 3), Fenton shale.

Fig. 10, var. *reinschi* nov., holotype, ×250.

Fig. 11, var. *mediolobatus* nov., holotype, ×250.

Remarks. The spores which have previously been described as *S. intortus* are all included in this variety. The size limits of our examples, based on the measurement of twenty-three specimens, were 66–110 μ; the mean was 79·5 μ, and the standard deviation 14·0 μ. Reinsch (1884) figured many spores which are comparable to *S. intortus* var. *intortus*. These were included in the subdivisions VIII and XIV of subfamily 1 (nucleus triangularis) and are listed here: pl. 4, figs. 45, 47, 48, 51, 51A, 54; pl. 5, fig. 58; pl. 6, figs. 77 (right-hand figure), 80, 84, 86; pl. 15, figs. 48A, 51B (given as 51A in explanation of plates), 59A; pl. 18, fig. 106A; pl. 19, fig. 45B; pl. 49B, figs. 1, 6–8. Their dimensions ranged from 35–105 μ. Many of the above forms were assigned by Horst (1955, p. 184) to *S. intortus*. In the description of subdivision XIV Reinsch states 'exosporium bi-tri-lamelosum' which in some cases probably indicates a differentiated cingulum.

The type 4K of Knox (1942, fig. 4, p. 6; 1947, fig. 45) from the Limestone Coal Group of Northumberland and Fife, and the Middle Coal Measures of Cumberland resembles *S. intortus* var. *intortus*.

Occurrence. Karaganda Basin, Russia (after Luber and Waltz 1938), Tournaisian–Viséan. Central Russia (after Reinsch 1884), Carboniferous. Western Upper Silesia (after Horst 1955), Westphalian A. Moravska Ostrava (after Horst 1955), Namurian B. Fife and Northumberland (after Knox 1942, 1947), Lower Carboniferous. Cumberland (after Knox 1942), Westphalian. Yorkshire, Middle Fenton Cannel Coal and shale, Upper Westphalian A; Barnsley Seam, Middle Westphalian B. Flintshire, Cannel Coal, Middle Westphalian A.

Simozonotriletes intortus var. *fentonensis* nov.

Plate 26, figs. 5–6; text-fig. 3

Holotype. Slide M1B4 ref. 250847 in the collection of the Geology Department, Sheffield University, from Middle Fenton Cannel Coal, Coldbath opencast site, near Barnsley, Yorkshire. Upper Westphalian A.

Diagnosis. Size 85–95 μ, holotype 88 μ; triangular in equatorial outline with convex or concave sides and rounded apices; dark zone of cingulum is of constant thickness, but tends to be wider at the apices.

Description. Colour yellow, dark zone brown. Equatorial outline is triangular with convex or concave sides and rounded apices. Central area often corroded, exine finely infrapunctate to infragranulate. Trilete rays about $\frac{3}{4}$ radius of central area. Cingulum is differentiated into dark and light zones. Inner margin of dark zone is irregular in outline, but tends to be wider at the apices where it may overlap on to the central area. Apices not thickened.

Comparison and remarks. In *S. intortus* var. *intortus* the dark zone maintains a uniform width and thickness around the equator. A total of nine specimens were assigned to *S. intortus* var. *fentonensis*; the mean was 92 μ, and the standard deviation 5 μ. The name *fentonensis* is used to denote the horizon of the type material.

Occurrence. Middle Fenton Cannel Coal and shale, Upper Westphalian A.

Simozonotriletes intortus var. *lineatus* nov.

Plate 26, figs. 7–9; text-fig. 4

Holotype. Slide M2E4 ref. 258748 in the collection of the Geology Department, University of Sheffield, from shale above the Middle Fenton Seam, Coldbath opencast site, near Barnsley, Yorkshire. Upper Westphalian A.

Diagnosis. Size 75–90 μ, holotype 85 μ, triangular in equatorial outline with straight sides; dark zone continuous along the interradial margins, apices variously thickened; width of dark zone to radius of central area is about 1:1 to 1:2.

Description. Colour yellow, dark zone brown. Equatorial outline triangular with almost straight sides. Trilete rays extend to margin of central area, exine infrapunctate. Cingulum differentiated into dark and light zones, dark zone thickened and sometimes expanded at the apices. Thickening not uniform and may be more pronounced in one of the valvae.

Comparison and remarks. In *S. intortus* var. *polymorphosus* the sides are usually more concave, the dark zone less well defined in interradial regions, and the valvae tend to be larger. The dark zone is not thickened at the apices in *S. intortus* var. *fentonensis*. The size limits of this variety are erected on the measurement of seven specimens. The calculated mean and standard deviation were 82 μ and 4 μ respectively. The name *lineatus* is used to indicate the straight sides which are characteristic of this variety.

Occurrence. Middle Fenton Cannel Coal and shale, Upper Westphalian A.

Simozonotriletes intortus var. *sublobatus* (Waltz)

Plate 26, figs. 10–12; text-figs. 5*a*, *b*

Zonotriletes sublobatus Waltz *in* Luber and Waltz 1938, p. 17, pl. 2, fig. 22.
Simozonotriletes sublobatus (Waltz), Potonié and Kremp 1956*a*, p. 110.

Holotype. Plate 2, fig. 22 of Luber and Waltz (1938). *Figured material*. Slides M1B4 (144639), M1B5 (358698), M1B1 (258791), M2E4 (169767) in the collection of the Geology Department, University of Sheffield, from the Middle Fenton Cannel Coal and shale, Coldbath opencast site, near Barnsley, Yorkshire. Upper Westphalian A.

Diagnosis. Size 35–80 μ, holotype (measured from figure) approximately 60 μ; cingulum displays no clear differentiation into dark and light zones, and is wider and thicker at the apices.

Description. Colour yellow to brown. Triangular in equatorial outline with straight to concave sides and rounded apices. Central area outline may be indistinct, exine levigate to infrapunctate. Trilete rays exceed $\frac{3}{4}$ radius of central area, suture usually closed. The cingulum shows no clear differentiation into dark and light zones in the interradial region, and is expanded and thickened at the apices. Thickening is irregular and may be more marked at one apex. Inner margin of the valvae sometimes overlap on to the central area.

Comparison and remarks. The differential thickening of the cingulum is not as marked as in *S. intortus* var. *polymorphosus*. The dimensions of the forms found by Waltz, and described under *Zonotriletes sublobatus*, ranged from 37·5 to 60 μ. He noted that the cingulum was smooth, and thickened and expanded at the apices. To conform with the original diagnosis *S. intortus* var. *sublobatus* is now restricted to forms in which the undifferentiated cingulum is wider and thicker at the apices. The maximum diameter of fourteen specimens obtained from the Fenton horizon varied between 66·5 and 80 μ. They possessed a mean diameter of 73 μ, and had a standard deviation of 5 μ. The figure of Reinsch (1884, pl. 6, fig. 77) was referred by Waltz to his species *Zonotriletes sublobatus*. The spore figured in Reinsch (1884, pl. 3, fig. 34) is also included here.

Occurrence. Karaganda Basin, Russia (after Luber and Waltz 1938), Tournaisian–Viséan. Pruckscha, central Russia (after Reinsch 1884), Carboniferous. Middle Fenton Cannel Coal and shale, Upper Westphalian A.

Simozonotriletes intortus var. *polymorphosus* nov.

Plate 27, figs. 1–12; text-figs. 7*a–f*

Holotype. Slide M2E7a ref. 196712 in the collection of the Geology Department, University of Sheffield, from the shale above the Middle Fenton Seam, Coldbath opencast site, near Barnsley, Yorkshire. Upper Westphalian A.

Diagnosis. Size 60–100 μ, holotype 81·5 μ; apices thickened, cingulum in interradial regions may be homogeneous or differentiated into dark and light zones; dark zones, if present, are usually absent from one or more of the sides.

Description. Colour yellow, valvae brown. Equatorial outline triangular with straight to concave sides and rounded apices. Central area outline distinct, exine levigate to infrapunctate. The trilete rays exceed $\frac{3}{4}$ of the radius of the central area. Apical regions of the cingulum are thickened, the form of the valvae being dependent on the configuration of the apices. The inner boundary of the valvae may overlap on to the central area (e.g. Pl. 27, fig. 12).

Comparison and remarks. In *S. intortus* var. *concavus* the sides are more concave, the apices more rounded, and the cingulum tends to be narrower along the margins. In *S. intortus* var. *lineatus* there is a well-defined dark zone between the valvae. *S. intortus* var. *polymorphosus* was the dominant variety present in the Fenton assemblages. A total of thirty specimens were recognized, having a mean and standard deviation of 83 μ and 7·5 μ. The spore on pl. 6, fig. 79 of Reinsch (1884) resembles *S. intortus* var. *polymorphosus*. The name *polymorphosus* is used to indicate the wide variation displayed by forms assigned to this variety.

Occurrence. Zwickau, Saxony; and Towarkowa, central Russia (both after Reinsch 1884), Carboniferous. Middle Fenton Cannel Coal and shale, Upper Westphalian A.

Simozonotriletes intortus var. *concavus* nov.

Plate 28, figs. 1–2; text-fig. 8

Holotype. Slide M1B2 ref. 342845 in the collection of the Geology Department, University of Sheffield, from the Middle Fenton Cannel Coal, Coldbath opencast site, near Barnsley, Yorkshire. Upper Westphalian A.

Diagnosis. Size 60–90 μ, holotype 80 μ; sides concave, apices broad and rounded, cingulum in interradial regions is narrow (up to about 8 μ), and expanded and thickened into valvae at the apices; inner lines of valvae may overlap on to the central area.

Description. Colour yellow, apices brown. Triangular in equatorial outline with concave sides and broad rounded apices. Exine of central area is infrapunctate to infragranulate, rays frequently open and are about $\frac{3}{4}$ radius of central area. Valvae are present at the apices which may be joined by a narrow, ill-defined dark zone along one or more of the interradial regions.

Comparison and remarks. In *S. intortus* var. *trivalvis* the valvae are more prominent and there is no dark zone along the margins. The mean and standard deviation of the five specimens included in this variety were 73·5 μ and 8·5 μ respectively. The figure of Reinsch (1884, pl. 6, fig. 78) is probably *S. intortus* var. *concavus*. The varietal name denotes the concave sides characteristic of the forms included here.

Occurrence. Malowka, central Russia (after Reinsch 1884), Carboniferous. Middle Fenton Cannel Coal and shale, Upper Westphalian A. Barnsley Coal, Middle Westphalian B.

Simozonotriletes intortus var. *trivalvis* (Waltz)

Plate 28, fig. 3; text-figs. 9*a*, *b*

Zonotriletes trivalvis Waltz *in* Luber and Waltz 1938, p. 18, pl. 4, fig. 41.
Triquitites trivalvis (Waltz), Potonié and Kremp 1956*a*, p. 88.

Holotype. Plate 4, fig. 41 of Luber and Waltz (1938), reproduced here as text-fig. 9*a*.
Figured material. Slide M2E7b ref. 460653 in the collection of the Geology Department of the University of Sheffield, from the Middle Fenton shale, Coldbath opencast site, near Barnsley, Yorkshire. Upper Westphalian A.

Diagnosis. Size 45–80 μ, holotype (measured from figure) approximately 65 μ; equatorial outline trefoil in shape with markedly concave sides and prominent apices; three equatorial auriculae lie opposite the angles of the central area; the remainder of the equatorial region unthickened.

Description. Colour yellow, auriculae brown. Triangular in transverse plane, sides concave, apices broad and well rounded. Margin of central area less concave, exine levigate to finely infrapunctate. The trilete rays are distinct and exceed $\frac{3}{4}$ radius of central area. The auriculae are smooth, pad-like thickenings of the exine. The structureless, unthickened equatorial region is narrow along the interradial margins and may be absent at the apices.

EXPLANATION OF PLATE 26

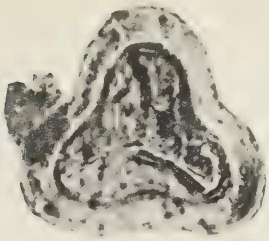
All figures × 500

Figs. 1–4. *Simozonotriletes intortus* var. *intortus* (Waltz). 1, Fenton cannel coal, slide M2C1d ref. 152831—66·5 μ. 2, Barnsley coal, slide M9A3 ref. 355654—107 μ. 3, Fenton cannel coal, slide M2C1c ref. 295786—71 μ. 4, Fenton shale, slide M2E7a ref. 168719—66·5 μ.

Figs. 5–6. *Simozonotriletes intortus* var. *fentonensis* nov. 5, Holotype, Fenton cannel coal, Slide M1B4 ref. 250847—88 μ. 6, Fenton cannel coal, slide M2C1f ref. 261796—93 μ.

Figs. 7–9. *Simozonotriletes intortus* var. *lineatus* nov. 7, Holotype, Fenton shale, slide M2E4 ref. 258748—85 μ. 8, Fenton shale, slide M2E2 ref. 221812—83 μ. 9, Fenton shale, slide M2E7a ref. 158817—84 μ.

Figs. 10–12. *Simozonotriletes intortus* var. *sublobatus* (Waltz). 10, Fenton cannel coal, slide M1B4 ref. 144639—83 μ. 11, Fenton cannel coal, slide M1B5 ref. 358698—75 μ. 12, Fenton cannel coal, slide M1B1 ref. 258791—76 μ.



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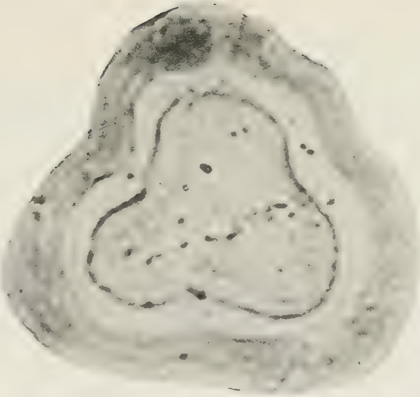

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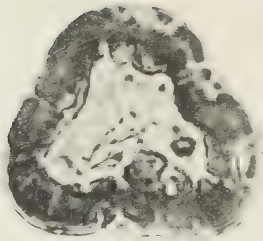

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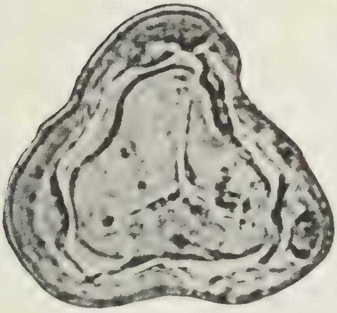

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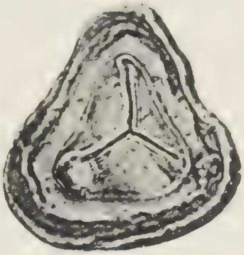

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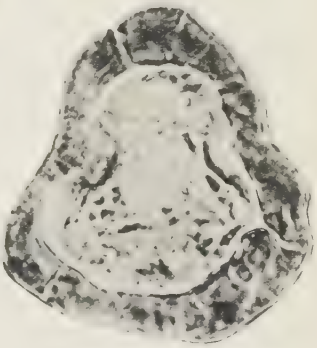

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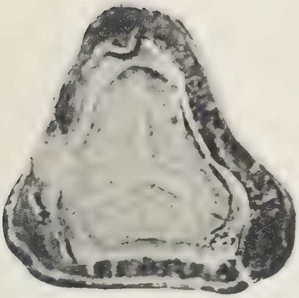

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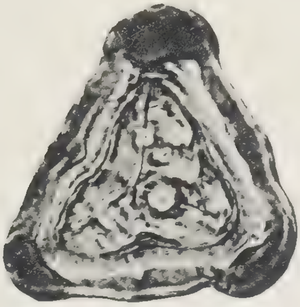

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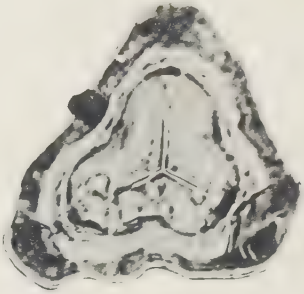

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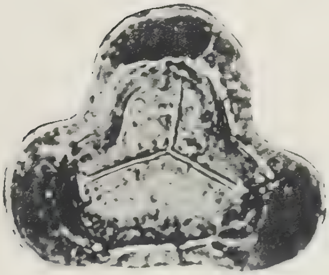

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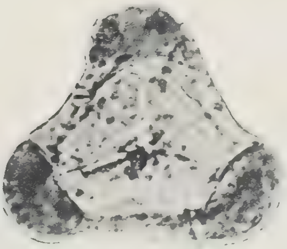

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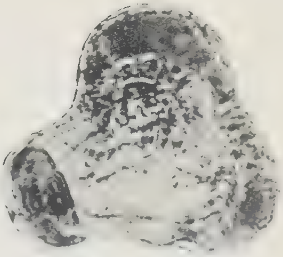

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SULLIVAN, *Simozonotriletes*

Comparison and remarks. S. intortus var. *trivalvis* resembles *S. intortus* var. *concavus*, but the auriculae are larger and more prominent. Although represented by only two specimens in the Fenton assemblages, their distinctive nature warranted varietal discrimination. The morphological characters they displayed were in complete harmony with the original diagnosis of *Z. trivalvis* Waltz. The maximum diameters of the two spores were 76 μ and 80 μ.

Potonié and Kremp (1956*a*, p. 88) placed this form in *Triquitites* Wilson and Coe. The auriculae are similar in construction to those of *Triquitites*, but the presence of a well-defined central area obviates its inclusion in that genus. The specimen figured by Reinsch (1884, pl. 24, fig. 79D) was referred by Waltz to his species *Z. trivalvis.*

Occurrence. Karaganda Basin, Russia (after Luber and Waltz 1938), Tournaisian–Viséan. Central Russia (after Reinsch 1884), Carboniferous. Middle Fenton shale, Upper Westphalian A.

Simozonotriletes intortus var. *reinschi* nov.

Plate 28, figs. 4–9; text-fig. 10

Holotype. Slide M2E7b ref. 465792 in the collection of the Geology Department, University of Sheffield, from the shales above the Middle Fenton Seam, Coldbath opencast site, near Barnsley, Yorkshire. Upper Westphalian A.

Diagnosis. Size 75–90 μ, holotype 91 μ; thickened areas present along the interradial margins which may extend as narrow bands over the proximal and distal surfaces of the central area; width of cingulum is $\frac{1}{2}$–$\frac{2}{3}$ radius of the central area; extrema lineamenta sinuous.

Description. Equatorial outline triangular with slightly concave or convex sides and rounded apices. Cingulum differentiated into an outer dark zone and inner light zone. Dark zone often expanded and thickened at the apices. The presence of thickened areas in the interradial regions of the spore is diagnostic of this variety. The thickening may originate in the dark zone (e.g. Pl. 28, figs. 4, 6; text-fig. 10), or at the junction of the cingulum and central area (Pl. 28, fig. 7). In some forms the thickening continues on to the proximal and distal surfaces of the central area; in the holotype (Pl. 28, fig. 4; text-fig. 10) the thickened bands extend to points above and below the intersection of the trilete rays.

Remarks. The mean diameter of the six specimens referred to this variety was 84·5 μ and the standard deviation 3·5 μ. Reinsch, to whom this variety is dedicated, figured (1884, pl. 17, fig. 79C) a specimen from the 'Blatterkohle', Malowka, central Russia, which shows thickened areas in the dark zone of the cingulum.

Occurrence. Malowka, central Russia (after Reinsch), Carboniferous. Middle Fenton Cannel Coal and shale, Upper Westphalian A.

Simozonotriletes intortus var. *mediolobatus* nov.

Plate 28, figs. 10–12; text-fig. 11

Holotype. Slide M2E7b ref. 248685 in the collection of the Geology Department, University of Sheffield, from the shale above the Middle Fenton Seam, Coldbath opencast site, near Barnsley, Yorkshire. Upper Westphalian A.

Diagnosis. Size 60–90 μ, holotype 81·5 μ; cingulum in interradial regions is inciso-lobate; width of cingulum to radius of central area is in the ratio 1:3 to 2:5.

Description. Equatorial outline triangular with almost straight sides. Apices are rounded and sometimes thickened. The cingulum is differentiated into an inner light zone and outer dark zone. The equatorial margin is broken up into a number of lobate structures.

Comparison and remarks. *S. intortus* var. *mediolobatus* and var. *reinschi* are both characterized by complications of the cingulum along the interradial margins. The size limits of this variety were erected on the measurement of five specimens. The mean diameter was 74·5 μ and the standard deviation 10·5 μ. The name refers to the lobate nature of the margin.

Occurrence. Middle Fenton Cannel Coal and shale, Upper Westphalian A.

GENERAL DESCRIPTION OF THE VARIATION

The study of the variation has been concerned with the structure of the equatorial region, the shape of the spore in proximo-distal orientation, and the nature of the central area. The general triangular shape and the presence of a well-defined, sculptureless central area with long simple trilete rays are features shared by all the spores, and can be taken as indicative of their specific indentity. The modifications of the cingulum, although producing a wide variety of structures, do nevertheless take place along certain well-defined trends. The assemblages represent a continuously intergrading sequence of forms and it is solely for ease of reference and communication that the infraspecific categories are erected. The overall result of this gradation is to give rise to spores which display considerable differences in external form at the ends of several transitional series. Within the limits of the extreme examples any differentiation of the intermediate types is often a matter of conjecture and mainly dependent on the choice of a single variable character as the basis for subdivision. Such a character of prime importance in this particular group of spores is the cingulum, but the shape of the spore has been accorded a secondary role in the definition of the nomenclatural units.

The cingulum in its simplest case is a homogeneous equatorial border which is rounded at the equator and decreases in thickness towards the junction with the central area. A possible reconstruction is given in text-fig. 1. Spores which possess such a cingulum (Pl. 26, fig. 1; text-fig. 2*a*) are referred to *S. intortus* var. *intortus*; likewise the examples in which the dark and light zone of the cingulum maintain a constant width and thick-

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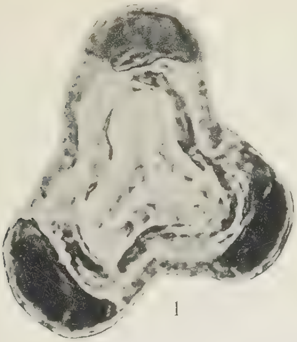
EXPLANATION OF PLATE 27

All figures ×500 unless otherwise stated

Figs. 1–12. *Simozonotriletes intortus* var. *polymorphosus* nov. 1, Fenton shale, slide M2E4 ref. 207665—92·5 μ. 2, Fenton shale, slide M2E7a ref. 445680—87 μ. 3, Fenton shale, slide M2E7a ref. 234730—86·5 μ. 4, Fenton shale, slide M2E6 ref. 325770—71·5 μ. 5, Fenton shale, slide M2E4 ref. 337726—87·5 μ. 6, Fenton shale, slide M2E6 ref. 238772—80 μ. 7, Fenton shale, slide M2E4 ref. 339778—73·5 μ. Note regular arrangement of hyphae-like structures on the central area. 8, Fenton shale, slide M2E4 ref. 273711—74 μ. 9, Fenton cannel coal, slide M1B3 ref. 311809—77 μ. 10, Holotype, Fenton shale, slide M2E7a ref. 196712—81·5 μ. 11, Fenton cannel coal, slide BM14 ref. 210763—76 μ. 12, Fenton shale, slide M2E6 ref. 238740—91 μ (×675).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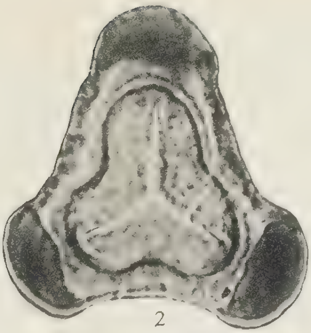
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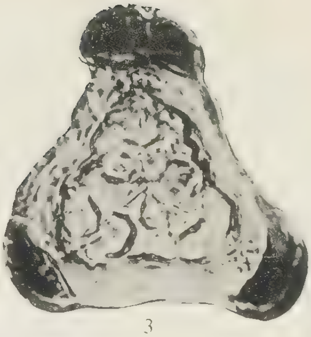
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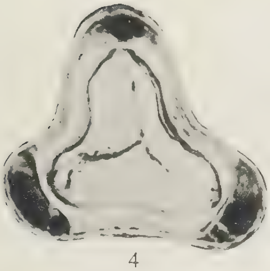
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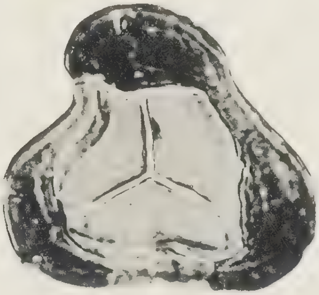
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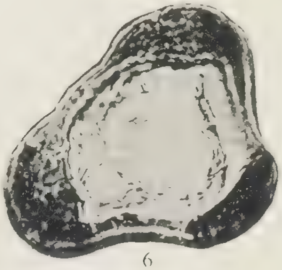
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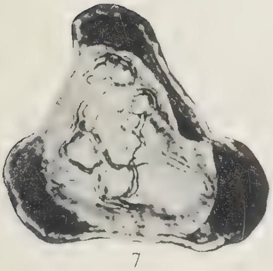
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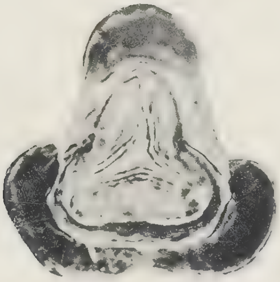
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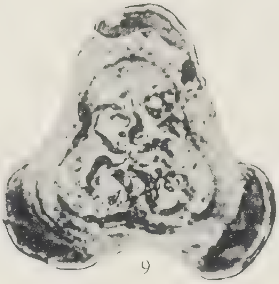
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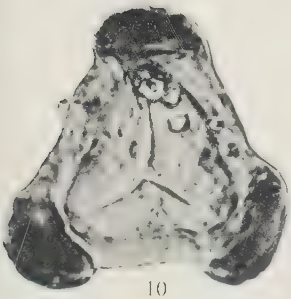
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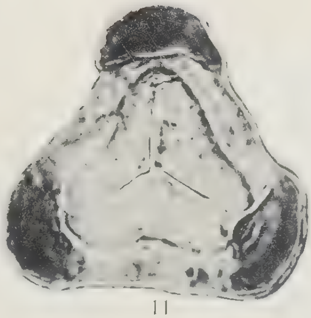
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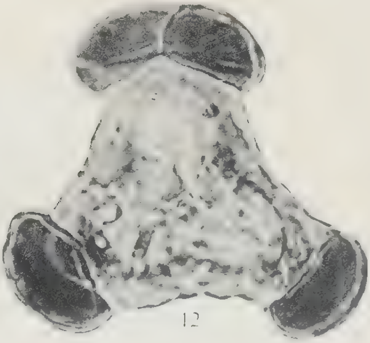
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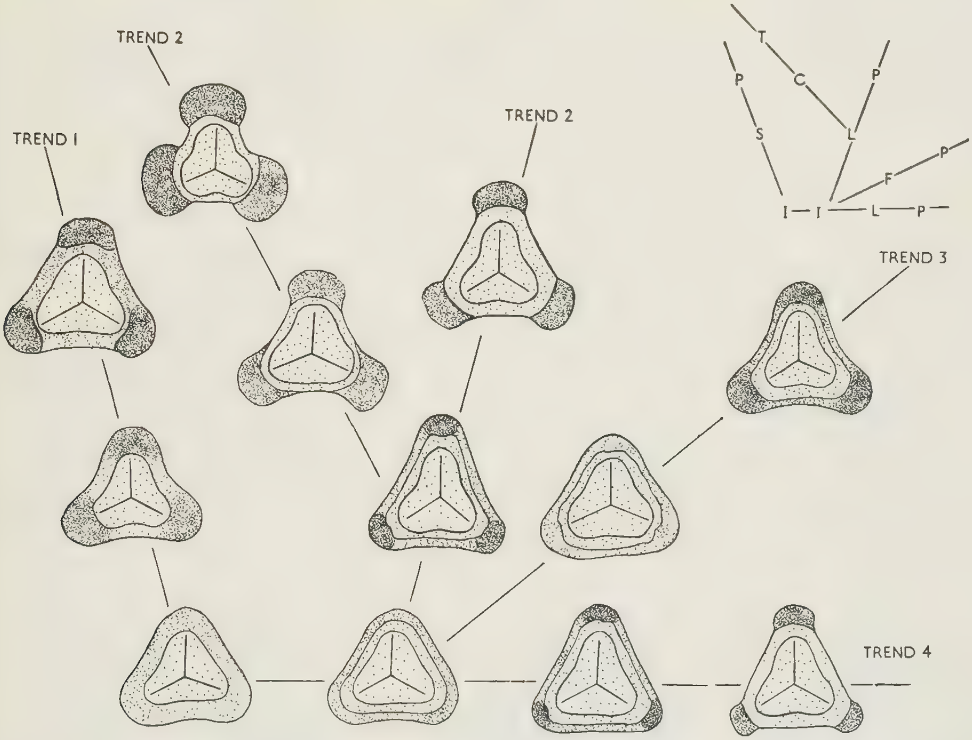
SULLIVAN, *Simozonotriletes*

ness around the equator (Pl. 26, fig. 2; text-fig. 2*b*), and those forms intermediate between the two (text-fig. 2*c*).

The overall pattern of variation displayed by the assemblages involved differential thickening of the cingulum. The principal trends were those leading to apical thickening, and are diagrammatically represented in text-fig. 12. From the evidence furnished by our examples this can arise in four possible ways:



TEXT-FIG. 12. Pictogram to illustrate the relationships of the varieties of *S. intortus* (Waltz) in four trends leading to apical thickening. The enumerated trends are described in the text. Key to insert diagram: I—*S. intortus* var. *intortus*; F—*S. intortus* var. *fentonensis*; L—*S. intortus* var. *lineatus*; S—*S. intortus* var. *sublobatus*; P—*S. intortus* var. *polymorphosus*; C—*S. intortus* var. *concavus*; T—*S. intortus var. trivalvis.*

(*a*) By localization of thickening at the expanded apices of an originally undifferentiated cingulum; trend 1 in text-fig. 12. The valvae of the specimens (Pl. 27, figs. 10, 11; text-figs. 7*a*, *f*) were probably derived from an undifferentiated cingulum.

(*b*) By an expansion and thickening of the dark zone at the apices, concomitant with a reduction in width and thickness along the margins; trend 2 in text-fig. 12.

(*c*) By expansion of the dark zone at the apices and reduction in interradial regions; trend 3 in text-fig. 12.

(*d*) By withdrawal of the dark zone between the apices; the amplitude of the valvae will then correspond to the original width of the dark zone, e.g. top apex of the spore in Pl. 27, fig. 9. Trend 4 in text-fig. 12.

The culmination of these trends is expressed by forms (Pl. 27, figs. 9, 12; text-fig. 7*a*) with three prominent valvae at the angles of an otherwise unthickened equatorial border. The variability of the shape of the valvae in a particular spore (e.g. Pl. 26, fig. 8; Pl. 27, fig. 3) is an indication that more than one of the four processes were operative during its development.

The progressive reduction in width and thickness of the dark zone along the margins is well illustrated in a series of forms assigned to *S. intortus* var. *polymorphosus*. The dark zone is continuous between the valvae in the specimens (Pl. 27, figs. 1, 4, 6; text-figs. 7*b*, *c*), but is absent from the lower border in the spore (Pl. 26, fig. 2), while in the example (Pl. 27, fig. 3) it is visible only as a narrow discontinuous band along the right-hand margin of the cingulum.

The rate of withdrawal of the dark zone is not necessarily uniform, and it may tend to persist along one or two of the sides (e.g. Pl. 27, figs. 7, 8). In a number of forms there would appear to be some relationship between the degree of development of the dark zone and the concavity of the sides (e.g. Pl. 27, fig. 8; text-fig. 7*c*).

The members of the *S. intortus* var. *concavus*–*S. intortus* var. *trivalvis* lineage are characterized by concave sides and broad, well-rounded apices. Forms referred to *S. intortus* var. *trivalvis* (Pl. 28, fig. 3; text-figs. 9*a*, *b*) represent the extreme expression of localized thickening at the apices.

Thickened areas are also present in the interradial regions, and this character becomes co-ordinated into the structures of the cingulum already described. In *S. intortus* var. *reinschi* (Pl. 28, figs. 4–9; text-fig. 10) the thickening usually originates in the dark zone of the cingulum, but in the spore (Pl. 28, fig. 7) a dark, semicircular area is situated at the junction of the cingulum and the central area. The specimen (Pl. 28, fig. 9) shows an early stage in the development of interradial thickening. Narrow bands may extend inwards from these thickened areas over the proximal and distal surfaces of the central area. In the spores (Pl. 28, fig. 4; text-fig. 10) they continue to points above and below the intersection of the trilete rays. The acquisition of the radial sculpture is reminiscent of the ornament found in other spore genera, e.g. *Knoxisporites* Potonié and Kremp 1954.

The outer margin of the cingulum is typically smooth to sinuous, but in the spores assigned to *S. intortus* var. *mediolobatus* it is incised along the interradial margins (Pl. 28, figs. 10–12; text-fig. 11). The dark zone is irregular in width due to the presence of the lobate projections.

Many of the forms described above have their counterparts in the spores illustrated by

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EXPLANATION OF PLATE 28

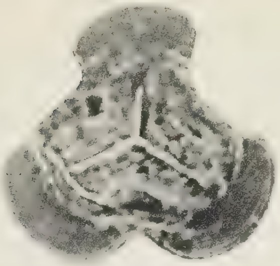
All figures × 500

Figs. 1–2. *Simozonotriletes intortus* var. *concavus* nov. 1, Holotype, Fenton cannel coal, slide M1B2 ref. 342845—80 μ. 2, Barnsley coal, slide M9A3 ref. 169735—63 μ.

Fig. 3. *Simozonotriletes intortus* var. *trivalvis* (Waltz). Fenton shale, slide M2E7b ref. 460653—80 μ.

Figs. 4–9. *Simozonotriletes intortus* var. *reinschi* nov. 4, Holotype, Fenton shale, slide M2E7b ref. 465792—91 μ. 5, Fenton shale, slide M2E7b ref. 342641—84·5 μ. 6, Fenton shale, slide M2E6 ref. 406740—83 μ. 7, Fenton cannel coal, slide M1B5 ref. 260663—87 μ. 8, Fenton shale, slide M2E4, ref. 279834—78 μ. 9, Fenton shale, slide M2E4 ref. 226762—83·5 μ.

Figs. 10–12. *Simozonotriletes intortus* var. *mediolobatus* nov. 10, Holotype, Fenton shale, slide M2E7b ref. 248685—81·5 μ. 11, Fenton cannel coal, slide M2C1a ref. 396699—86·5 μ. 12, Fenton shale, slide M2E1b 406745—60 μ.



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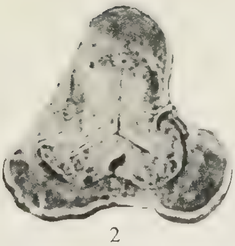

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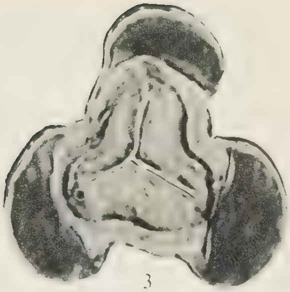

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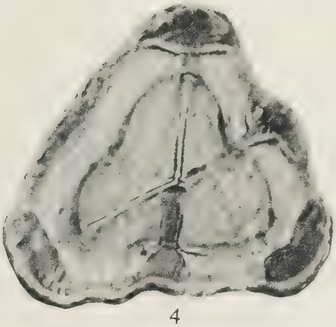

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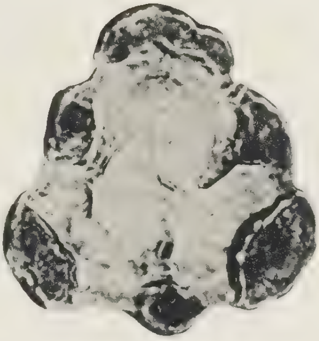

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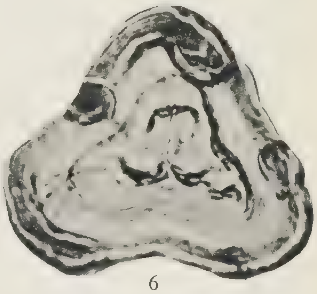

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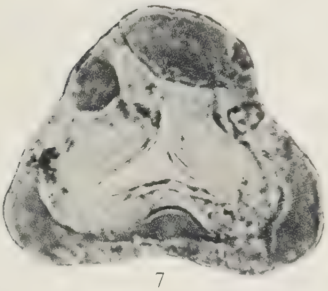

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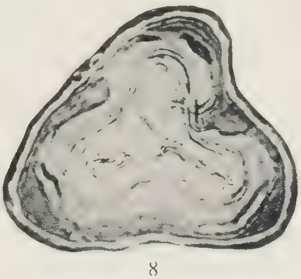

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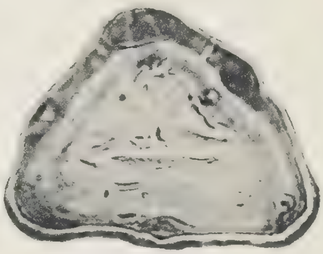

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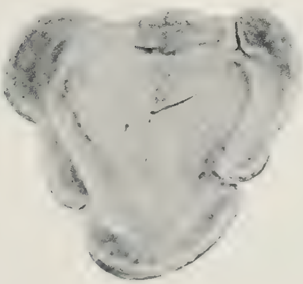

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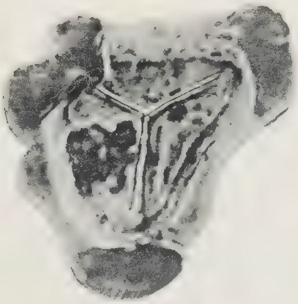

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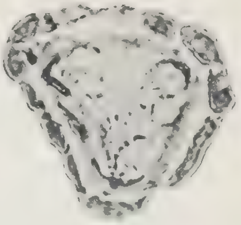

12

SULLIVAN, *Simozonotriletes*

Reinsch (1884), and this tempts an observation that the pattern of variation is simulated at other stratigraphical levels. However, the horizon of much of the material figured by Reinsch is not sufficiently well known to draw too close a comparison. Also the three species *Zonotriletes intortus*, *Z. sublobatus*, and *Z. trivalvis* described by Waltz *in* Luber and Waltz (1938) may well have represented a continuous morphological series.

SUMMARY OF STRATIGRAPHICAL DISTRIBUTION

The genus *Simozonotriletes* is known to have a widespread distribution in Europe and Asia. It has been found in Tournaisean-Viséan strata of the Karaganda Basin, Russia, by Luber and Waltz (1938); and at other localities in central Russia, mentioned by Reinsch (1884), in rocks the age of which cannot be ascertained more precisely than 'Carboniferous'.

In south-eastern Europe *S. intortus* has been identified by Horst (1955, p. 184) in the Prokop Coal (Namurian B), Upper Silesia; and in Seam VI Rudaer Schichten (Westphalian A) of Moravska Ostrava. The type 4K of Knox (1942, 1947), now equated with *S. intortus* var. *intortus*, appears in the Lower Carboniferous of Fife and Northumberland, and the Middle Coal Measures of Cumberland. *Simozonotriletes* has been described from Canada by Summers as *Muraspora.*

Simozonotriletes is dominantly a Lower Carboniferous and Namurian genus, and Potonié and Kremp (1954, p. 159; 1956*a*, p. 109) have gone so far as to state 'Tournai-Visé bis Namur B, vielleicht nicht höher', and have indicated no Westphalian occurrences on their distribution charts (1954, p. 184; 1956*b*, p. 89). The spores found in this investigation extend up to Middle Westphalian B, and *Simozonotriletes* is thus shown to have a greater vertical range than had previously been supposed. Its sporadic appearance in rocks of Westphalian age, coupled with a distinctive morphology, may serve to establish this spore as an important stratigraphical index.

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THE UPPER LLANDOVERY TRILOBITES OF THE TORTWORTH INLIER, GLOUCESTERSHIRE

by M. L. K. CURTIS

ABSTRACT. Six species of trilobites from the Upper Llandovery rocks of the Tortworth Inlier are described and figured, including one new species, *Proetus asaphoides*.

INTRODUCTION

THE Upper Llandovery fauna of the Tortworth Inlier is a shelly one, consisting predominantly of brachiopods; the corals, molluscs, and trilobites form important but much less conspicuous elements. Of the trilobites fewer than ten species are known, and the only common forms are *Encrinurus onniensis* and *Dalmanites weaveri*. In the present paper the following species are described: *Calymene sp.*, *Proetus asaphoides* sp. nov., *Proetus sp.*, *Encrinurus onniensis* Whittard, *Phacops* cf. *orestes* Billings, and *Dalmanites weaveri* (Salter). Three other species, *Calymene replicata* Shirley, *Warburgella* cf. *stokesi* (Murchison), and *Arctinurus sp.*, are recorded, but are represented by poorly preserved material which provides no new information. The specimens studied are in the Geological Survey Museum, London (GSM), the Sedgwick Museum, Cambridge (SM), and the Geology Department of the University of Bristol.

Stratigraphy. The Upper Llandovery succession as developed in the Tortworth area consists of about 700 feet of fine-grained sandstones and shales belonging to the highest zones of the Series. These strata are divided into the Damery Beds below, which are fossiliferous throughout, and the Tortworth Beds above, which contain the highly fossiliferous *Palaeocyclus* Band at their base; the two groups are separated on the eastern side of the inlier by the Upper Trap, an extrusive lava (Reed and Reynolds 1908, pp. 513–22; Curtis 1955, pp. 5–6).

Acknowledgements. I wish to express my sincere thanks to Professor W. F. Whittard for his help and encouragement, to Dr. C. J. Stubblefield and Mr. A. G. Brighton for the loan of specimens from the Geological Survey and Sedgwick Museums respectively, and to Mr. E. W. Seavill for photographing the specimens. The award of a Graduate Scholarship by the University of Bristol is gratefully acknowledged.

DESCRIPTIONS OF SPECIES

Family CALYMENIDAE Edwards 1840

Calymene sp.

Plate 29, fig. 1

Description. Pygidium is markedly convex. Six rings are visible in the axis, but there would probably be eight or nine in a complete pygidium; an unsegmented posterior part of the axis is as long as the three preceding rings. Deep axial furrows coalesce posteriorly

[Palaeontology, Vol. 1, Part 2, 1958, pp. 139–146, pl. 29.]

to produce a somewhat angulated termination to the axis. Pleurae, of which there are five pairs, are separated by deep rib furrows, and become divided laterally by strong pleural furrows.

Horizon and locality. A single specimen (GSM 90030) was obtained in loose material derived from the Damery Beds at the western end of Ironmill Grove, Damery.

Affinities. The pygidium is narrower and has more axial rings than the form figured by Salter (1865, pl. 9, fig. 1*b*) from Bog Mine, near Shelve, Shropshire, which probably belongs to *Calymene planicurvata* Shirley (1936, p. 412). It is close to a pygidium from the Llandovery rocks of Mulloch, near Girvan (Salter 1865, pl. 9, fig. 2*b*), and also to that of *Calymene intermedia* var. *antigonishensis* McLearn (1924, p. 162, pl. 26, figs. 5–11) from the Stonehouse Formation of Arisaig, Nova Scotia.

Family PROETIDAE Hawle and Corda 1847

Proetus asaphoides sp. nov.

Plate 29, fig. 2

Description. A large and unusual species of *Proetus* is represented by a single incomplete and slightly distorted internal mould, measuring about 55 mm. from the front of the glabella to the posterior margin of the pygidium. Cephalon is imperfectly preserved. Glabella, which is convex and somewhat oval in form, narrows anteriorly and apparently bears no trace of glabellar furrows. Moderately strong furrows separate the occipital ring and occipital lobes from the rest of the glabella; the occipital ring curves forward at the centre, and is separated from the relatively large sub-triangular occipital lobes by shallow and rather indistinct furrows. A fragment of the posterior border of the fixed cheek is preserved, and shows that the pleuroccipital furrow meets the axial furrow at the level of the occipital lobe.

Thorax consists of ten segments. Axis is convex and only slightly tapering; the central portion of each axial ring is broken away showing the articulating half-ring of the succeeding segment. Pleural lobes are nearly flat, and the pleurae carry broad, shallow pleural furrows.

Pygidium is large, its length being considerably greater than that of the thorax. Axis is fairly strongly convex and tapers posteriorly. First axial ring is pronounced but short, and separated from the articulating half-ring by a strong groove. Posteriorly the axial rings are faintly marked, though there are indications of at least seven rings. Pleural lobe is gently convex. Pleurae, of which five are visible, consist of broad, low ridges, and are separated by shallow rib furrows. The lateral portion of the pleural lobe is missing, and exposes to view the external mould of the broad doublure with its fine terrace lines. In the region of the third and fourth pleurae the doublure is at least 4 mm. wide and is concave ventrally. Near the posterior end of the pygidium the doublure is more than 6 mm. wide; here it is concave ventrally near the axis, but postero-laterally it flattens and becomes slightly convex ventrally.

Holotype. GSM GSb 4687.

Horizon and locality. The holotype was obtained by Thomas Weaver in Cullimore's Trap Quarry, Charfield. The specimen is undoubtedly from the base of the Tortworth Beds, for the only sedimentary rocks occurring in Cullimore's Quarry are those which immediately succeed the Upper Trap. The account of the north-western part of Cullimore's Quarry given by Weaver (1824, p. 334, pl. 39, fig. 2) shows that in his time two fossiliferous bands were exposed, and these are referred to as layers 3 and 5. He states that the 'layers No. 3. and 5. contain numerous remains of caryophyllites, favosites, astreites, bivalves, etc., and I found also the impression of a trilobite'. Since no other mention is made of trilobite remains from Cullimore's Quarry, it seems probable that this is the specimen described here. It should be noted, however, that Weaver makes no mention of this form in his discussion of the trilobites (pp. 326–7).

Affinities. *Proetus asaphoides* (so named from the *Asaphus*-like pygidium) differs from most Silurian Proetids in possessing a large pygidium. It shows some resemblance to certain Devonian forms such as *Proetus rowi* (Green) from the Hamilton Group of North America (Hall and Clarke 1888, p. 119, pl. 21, figs. 2–6, 24–26; pl. 23, figs. 20–29) and *Proetus bohemicus* Hawle and Corda from Stage F of Bohemia (Barrande 1852, p. 452, pl. 16, figs. 1–15); in both these species, however, the pygidium is considerably smaller.

Proetus sp.

Plate 29, fig. 3

Description. Only the pygidium is known. In an internal mould (GSM 90031; Pl. 29, fig. 3*a*), measuring 4·5 mm. in length and 7·5 mm. in breadth, the axis is pronounced and elevated well above the level of the rather flat pleural lobes. Axis tapers and is rounded posteriorly. Axial rings, of which at least seven are visible, are strong and sharp, particularly the first three or four. Pleural lobes are gently convex and almost smooth, but show traces of the first, second, and third pleurae; near the margin the pleurae become distinct and here they carry broad pleural furrows. Running concentrically round the pygidium is a slight depression which coincides in position with the inner limit of the doublure. At the posterior margin the specimen is broken and exposes the mould of the external surface of the doublure, which is slightly convex ventrally, about 1 mm. wide, and carries fine terrace lines. A fragment of the external mould of the same individual remains (Pl. 29, fig. 3*b*), and here the axial rings and pleurae are more clearly defined than in the internal mould, and the pleurae are seen to carry distinct pleural furrows. The posterior margin of the pygidium is entire and is marked by a feebly developed upturned rim.

Horizon and locality. The form is known by two individuals, both of which are from the Damery Beds of the Damery Bridge area.

Affinities. The Tortworth specimens somewhat resemble *Proetus pseudolatifrons* Reed (1904, p. 78, pl. 11, figs. 7–9) from the Camregan Group of Girvan. They are closely similar, as regards the raised axis and rather smooth pleural lobes, to specimens from the Upper Silurian of the Harz, described by Kegel (1928, p. 634, pl. 32, figs. 1–5) as *Proetus conspersus* (Angelin).

Family ENCRINURIDAE Angelin 1854

Encrinurus onniensis Whittard

Plate 29, figs. 4–5

Calymene ?? punctata Murchison 1839, p. 661, pl. 23, fig. 8*a*.
Encrinurus onniensis Whittard 1938, p. 118, pl. 4, figs. 6–11.

Description. Although the Tortworth Encrinurids show much variation in minor characters, it is not possible to divide them into distinct and separate groups, and they are here considered as members of a single species. Some individuals are identical with *Encrinurus onniensis* Whittard (1938, p. 118, pl. 4, figs. 6–11), and consequently all the Tortworth Encrinurids are referred to that species.

Cephalon, which usually occurs in a fragmentary condition, agrees closely with the description of *E. onniensis*. Thorax is not known. It is in the pygidium that the variations are most apparent. Some pygidia are similar in every respect to those of *E. onniensis* described from Shropshire. Others are narrower and more strongly convex (Pl. 29, fig. 4), and in addition to tubercles on the axis, which occur on about every fourth or fifth ring, there are also tubercles on the pleurae; each pleura carries one tubercle, usually towards its inner end, but occasionally near the middle or even towards the outer end; as a rule the outermost tubercles occur on the first and fourth pleurae, but this is not always so. Between these two kinds—the typical *E. onniensis* on the one hand, and the more convex, tuberculate type on the other—come intermediate forms (Pl. 29, fig. 5).

Horizons and localities. The species is common in the Damery Beds at most localities, and also occurs in the *Palaeocyclus* Band at the base of the Tortworth Beds.

Family PHACOPIDAE Hawle and Corda 1847

Phacops cf. *orestes* Billings

Plate 29, fig. 6

Description. An external mould of the pygidium measures 5·5 mm. in length and 9 mm. in breadth (SM A 35410a). Axis is convex and consists of at least seven rings, but posteriorly they become indistinct. First axial ring is considerably broader than the rest; the third and succeeding rings curve forward slightly at the centre and also near the axial furrows, giving the ring furrows a wavy appearance. Five pairs of depressed pleurae are separated by narrow rib furrows which swing forward slightly against the axial furrows. Anterior pleurae, which carry feebly developed pleural furrows, extend about two-thirds of the distance to the margin, ending laterally against the wide smooth border. Articulating half-ring and facets are visible at the anterior end of the pygidium. In the internal mould of the same individual the smooth border is somewhat narrower, and the doublure is seen to be ventrally convex.

Horizon and locality. A single specimen has been obtained from the Damery Beds at Damery.

Affinities. The pygidium is almost identical with that of *Phacops orestes* Billings (1860, p. 65, figs. 10, 10*a*) which is common in the Gun River and Jupiter Formations of Anticosti Island (Twenhofel 1928, p. 335, pl. 50, figs. 11–12; Delo 1940, p. 21, pl. 1, figs. 22–25).

Family DALMANITIDAE Delo 1935

Dalmanites weaveri (Salter)

Plate 29, figs. 7–10

Phacops Weaveri Salter 1849, p. 7, pl. 1, fig. 16.
Phacops Weaveri Morris 1854, p. 114.
Phacops Weaveri Salter 1864, p. 57, pl. 3, fig. 1; pl. 4, figs. 6–7; (*non* pl. 3, figs. 2–3; pl. 4, figs. 8–9).
Phacops Weaveri Reed 1909, p. 69.
Dalmanites (*Dalmanitina*) *Weaveri* Reed 1909, p. 73.
?Dalmanites weaveri McLearn 1924, p. 169, pl. 27, figs. 7–10.
Dalmanitina weaveri Reed 1927, p. 341.
Dalmanites weaveri Whittard 1938, p. 132.
?Dalmanitina weaveri Delo 1940, p. 53, pl. 4, figs. 7–9; (*non* pl. 4, fig. 10).

Description. The following account of the cephalon is founded on an external mould, preserved in fine-grained sandstone, measuring 13 mm. in length and 22 mm. in breadth (GSM 90033; Pl. 29, fig. 7*a*).

Cephalon is convex, somewhat triangular in outline, and nearly twice as broad as long. Frontal lobe of the glabella is large and sub-rhomboidal; towards its posterior edge, and in the mid-line, is a small elongated pit. First glabellar furrows are deep, extend across the glabella, and are directed antero-laterally. Second and third glabellar furrows directed laterally, and represented by no more than a trace at the mid-line. Occipital ring curves forward at the centre and is elevated slightly above the level of the rest of the glabella, from which it is separated by a well-defined occipital furrow. Axial furrows diverge anteriorly and are slightly curved, being concave outwards. Each axial furrow follows round the anterior part of the eye, joins the first glabellar furrow, and curves outward to coalesce with the lateral border furrow. A feebly developed furrow extends round the anterior of the frontal lobe. Fixed cheek is convex and steepens considerably towards the palpebral lobe; postero-laterally the fixed cheek extends backwards to form a short fixigenal spine. Lateral border furrow meets the pronounced pleuroccipital furrow at the fixigenal angle whence an incipient furrow extends a short distance along the fixigenal spine. Free cheek is small; the lateral border furrow increases in width until it reaches the anterior end of the free cheek where it meets the first glabellar furrow. The course of the anterior branch of the facial suture is not clearly defined, but it appears to swing outward in front of the eye, and then probably continues round the anterior of the frontal lobe. Posterior branch of the facial suture swings forward behind the eye, but between the eye and the lateral border furrow it curves back and continues in a postero-lateral direction. Behind the eye, on the fixed cheek, is a short groove in which is situated the posterior branch of the facial suture. Eyes are prominent, being raised above the level of the rest of the cephalon. The upper part of the eye consists of a smooth, convex, crescentic area, separated from the palpebral lobe by a shallow groove. Visual surface is steep and curved, and near its centre attains a maximum 'height' of about 2·5 mm., but anteriorly and posteriorly it becomes narrower and has rounded ends; the surface is almost vertical at its posterior end, but anteriorly it slopes forward and outward at a steep angle. There are about thirty vertical rows of small facets which appear as sub-hexagonal concavities; the number of facets in each row diminishes from about nine in the central rows to two or three in the extreme anterior and posterior rows; the total number of facets in each eye is approximately 160. The internal mould of the cephalon (GSM 90033a, which is the counterpart of GSM 90033) differs but slightly from the external mould, the chief difference being that the furrows are shallower. Also, there are small subsidiary ridges in the deeper parts of the glabellar furrows and the occipital furrow (Pl. 29, fig. 7*b*); this feature, however, is only occasionally visible in internal moulds, and may be due to the shell at the base of the furrows having been broken or eroded through prior to fossilization. The ornamentation of the cephalon consists of delicate tubercles, and is seen in a cranidium preserved in limestone (Pl. 29, fig. 8).

The holotype is a small pygidium measuring 6·5 mm. in length and 8·5 mm. in breadth, and showing a marked convexity (Pl. 29, fig. 9). Axis is about 2·7 mm. wide at its anterior end, but tapers gradually and has a rounded posterior termination. Twelve or thirteen axial rings are visible; those towards the anterior end are strongly developed, curve forward slightly at the centre, and are separated by wide ring furrows which are shallow at the mid-line but become deep towards the sides of the axis. Rings become less pronounced as traced in a posterior direction, the last few rings being indistinct. Axis is separated from the pleural lobes by well-marked axial furrows. There are seven distinct pairs of pleurae, but a further feebly developed pair is just visible. Anterior pleurae are strong and carry faint pleural furrows, but posteriorly the pleural furrows are apparently undeveloped. Pleurae are separated by broad rib furrows and end laterally against a smooth border which is about ½ mm. wide. At the posterior extremity of the pygidium is a small rounded point which is possibly an incipient terminal spine.

Most other pygidia examined are larger and less convex than the holotype which may be an immature individual. A more typical specimen is an internal mould measuring 11 mm. in length and about 15 mm. in breadth, and having eight pairs of pleurae (GSM

EXPLANATION OF PLATE 29

Fig. 1. *Calymene sp.* Internal mould of pygidium (GSM 90030), ×1·5. Damery Beds; loose material at western end of Ironmill Grove, Damery, near Tortworth.

Fig. 2. *Proetus asaphoides* sp. nov. Internal mould of holotype (GSM GSb 4687), ×1·5. Base of Tortworth Beds; Cullimore's Trap Quarry, Charfield.

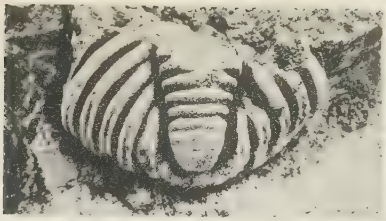
Figs. 3*a*, *b*. *Proetus sp.* 3*a*, Internal mould of pygidium, damaged at the posterior margin and showing the external mould of the doublure (GSM 90031), ×3. Damery Beds; loose material at extreme western end of Damery Quarry, 150 yards west 30° north of Damery Bridge, near Tortworth. 3*b*, Cast in latex of fragment of external mould of the same individual (GSM 90031b), ×3.

Figs. 4–5. *Encrinurus onniensis* Whittard. 4, Internal mould of pygidium (SM A 29519), ×3. Damery Beds; Avening Green, near Tortworth. 5, Internal mould of pygidium (GSM Geol. Soc. Coll. ρ 42), ×3. Figured by Murchison 1839, pl. 23, fig. 8*a*. Damery Beds; Micklewood Chase, near Tortworth.

Fig. 6. *Phacops* cf. *orestes* Billings. Cast in latex of external mould of pygidium (SM A 35410c), ×3. Damery Beds; Damery, near Tortworth.

Figs. 7–10. *Dalmanites weaveri* (Salter). 7*a*, Cast in latex of external mould of cephalon (GSM 90033b), ×2. Damery Beds; roadside section about 60 yards south of Damery Bridge, near Tortworth. 7*b*, Part of internal mould of glabella of the same individual showing small subsidiary ridges within the glabellar and occipital furrows (GSM 90033a), ×4. 8, Portion of exterior of frontal lobe of glabella showing fine tuberculate ornamentation; specimen preserved in limestone (GSM 90032), ×10. Damery Beds; Damery, near Tortworth. 9, Internal mould of pygidium (GSM GSd 3154), ×3. Holotype, figured by Salter 1849, pl. 1, fig. 16. Damery Beds; Long's Quarry, Charfield. 10, Internal mould of pygidium (GSM 19221), ×2. Topotype, figured by Salter 1864, pl. 4, fig. 7. Damery Beds; Long's Quarry, Charfield.

Photographs by Mr. E. W. Seavill.



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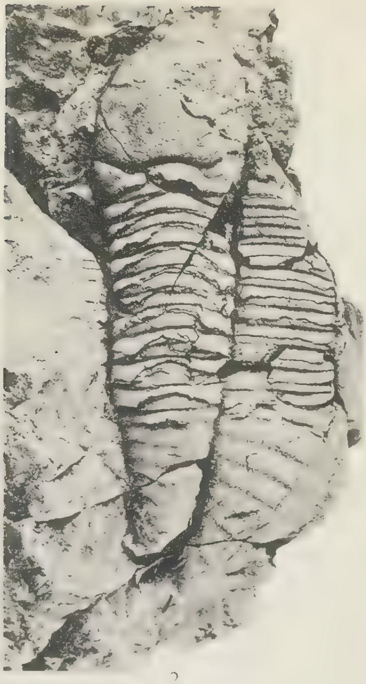

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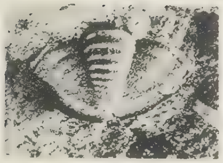

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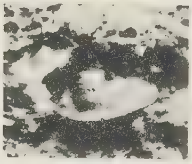

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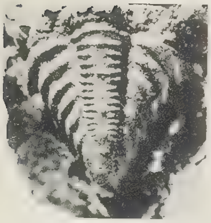

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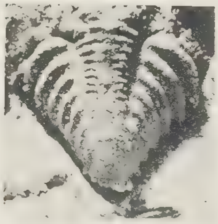

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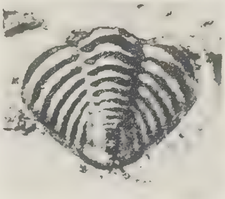

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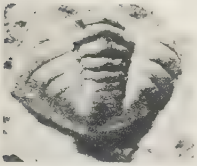

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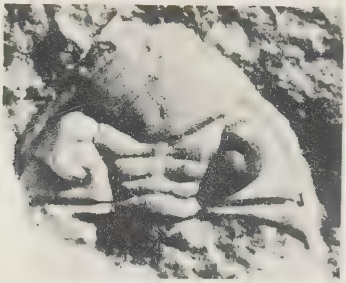

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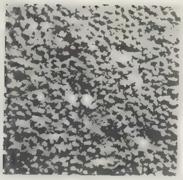

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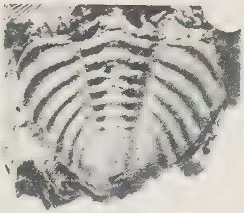

10

7b

CURTIS, Llandovery trilobites

19221; Pl. 29, fig. 10). The specimen is damaged at the posterior margin, but clearly shows the mould of the external surface of the doublure which is ventrally convex and about 1 mm. wide. Some internal moulds show small subsidiary ridges within the deeper parts of the ring furrows of the axis, similar to those described as occurring in the glabellar furrows, and in some pygidia there is a short but distinct terminal spine.

Holotype. GSM GSd 3154. This specimen, which was collected by Thomas Weaver from the Damery Beds in Long's Quarry, Charfield, is undoubtedly the original from which Salter's figure was drawn (see note by Whittard 1938, pp. 132–3).

Horizons and localities. The species occurs commonly at most localities in the Damery Beds and in the *Palaeocyclus* Band at the base of the Tortworth Beds.

Affinities. The form is similar to *Dalmanites weaveri* var. *tenuimucronata* Whittard (1938, p. 130, pl. 5, figs. 11–14), particularly as regards the cephalon. The pygidium of this variety, however, carries a long terminal spine; it also has more clearly defined rib furrows and pleural furrows, and the smooth border is somewhat broader.

The specimen figured by Salter (1864, p. 57, text-fig. 15) from Ile Percé, Gaspé, Canada, is not *Dalmanites weaveri*, but a Lower Devonian form to which Clarke (1908, p. 129) has given the name *Dalmanites* (*Probolium*) *biardi*.

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BIOSTROMES IN THE NAMURIAN GREAT LIMESTONE OF NORTHERN ENGLAND

by G. A. L. JOHNSON

ABSTRACT. Recent research has shown that the base of the Great Limestone of northern England lies close to the junction between the Lower and Upper Carboniferous and this stratum has thus gained a new significance. The fauna and lithology of three biostromes, the *Chaetetes* Band, Brunton Band, and Frosterley Band, which occur persistently in the Great Limestone are described in detail. Two of these, the coralline *Chaetetes* Band and the algal Brunton Band are new; they are of widespread occurrence in northern England. The Frosterley Band (Dunham 1948) is mainly restricted to the Alston Block. A new fossil alga *Calcifolium bruntonense* sp. nov. is described and figured.

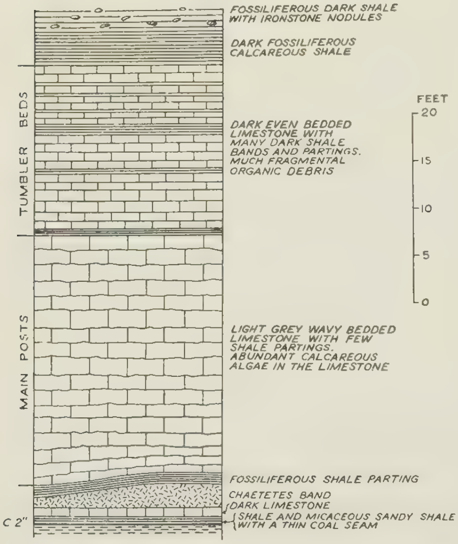
INTRODUCTION

THE presence of persistent biostromes in the Carboniferous Limestone of northern England was first described by Garwood (1913) whose '*Girvanella* Band' at the base of the D_2 Zone is perhaps the best known. Recently J. S. Turner (1956) has described faunal bands in the Yoredale Scar Limestone and Four Fathom Limestone of the Askrigg Block. The present paper concerns similar biostromes in the Yoredale Great Limestone which are particularly well developed on the Alston Block (northern Pennines). The bands consist of two coralline biostromes, one near the base and one near the centre of the limestone and an algal biostrome also near the centre of the limestone. The term biostrome means literally an organic layer and according to Cumings (1932, p. 334) they are by definition '. . . purely bedded structures, such as shell beds, crinoid beds, coral beds, etcetera, consisting and built mainly by sedentary organisms, and not swelling into moundlike or lenslike forms . . .'. The fossiliferous bands in the Great Limestone do lens to some extent but this is rarely perceptible and they are thus nearer true biostromes than bioherms; the former term is therefore retained in describing them.

The Great Limestone lies at the base of the Upper Limestone Group (Upper Bernician) of northern England and is a persistent and characteristic limestone member of a Yoredale type succession. To the south the Great (= Main) Limestone is known throughout the northern Pennines and northwards the Great (= Dryburn) Limestone has been traced to the Scottish Border (Gunn 1898; Trotter 1952; Rayner 1953). Throughout northern England the limestone lies at the top of a sequence of well-developed Yoredale cyclothems and underlies a rather different succession characterized by thick sandstones and grits with thin limestones; a faunal change also takes place in the vicinity of the Great Limestone. The lithological and faunal changes at this horizon led Stanley Smith (1910) to choose the base of the Great Limestone for the top of the D_2 Zone in Northumberland. Later Fowler (1926) adopted this horizon for the boundary between his Middle Limestone Group and Upper Limestone Group. This boundary has since been used satisfactorily in Northumberland, the Brampton district, Cumberland (Trotter and Hollingworth 1932), and the northern Pennines (Dunham 1948). The position of the Great Limestone in the Carboniferous zonal scheme has changed considerably since Smith's original work. The results of recent research are summarized by Rayner (1953)

[Palaeontology, Vol. 1, Part 2, 1958, pp. 147–157, pls. 30–31.]

who indicates that the Viséan–Namurian junction lies in the vicinity of the base of the Great Limestone. This boundary is a satisfactory junction between the Lower and Upper Carboniferous in northern England. Furthermore, it agrees with the Viséan–Namurian junction in Scotland where Currie (1954) has shown that it lies at the base of the Top Hosie Limestone on independent palaeontological evidence; the Top Hosie is equated with the Great Limestone with some certainty (Trotter 1952). The Great Limestone is now regarded as of basal E_1 age, Namurian.


FOSSILIFEROUS DARK SHALE WITH IRONSTONE NODULES
DARK FOSSILIFEROUS CALCAREOUS SHALE
TUMBLER BEDS
DARK EVEN BEDDED LIMESTONE WITH MANY DARK SHALE BANDS AND PARTINGS. MUCH FRAGMENTAL ORGANIC DEBRIS
FEET
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15
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0
MAIN POSTS
LIGHT GREY WAVY BEDDED LIMESTONE WITH FEW SHALE PARTINGS. ABUNDANT CALCAREOUS ALGAE IN THE LIMESTONE
FOSSILIFEROUS SHALE PARTING
CHAETETES BAND
DARK LIMESTONE
C 2"
SHALE AND MICACEOUS SANDY SHALE WITH A THIN COAL SEAM

TEXT-FIG. 1. Vertical section of the Great Limestone at Brunton Bank, Chollerford, near Hexham, Northumberland.

Acknowledgements. The writer wishes to acknowledge the assistance of Professor T. S. Westoll under whose guidance the initial research in Northumberland was conducted. He is indebted to Drs. H. Ll. L. Jones, A. J. Wells, and A. A. Wilson for supplying unpublished information on the biostromes, to Mr. J. S. Turner for demonstrating the presence of the biostromes in the upper Eden Valley area, and to Mr. G. F. Elliott and Dr. W. H. C. Ramsbottom for supplying the references to *Calcifolium*. Professor S. I. Tomkeieff greatly assisted in the translation of Russian literature and Professor K. C. Dunham has kindly checked the manuscript. Thanks are also due to the late Mr. G. W. O'Neill and to Mr. C. Chapman for help with the photography, and to Mr. A. Warne who prepared text-figs. 1 and 3 for publication.

FORM AND COMPOSITION OF THE GREAT LIMESTONE

The Great Limestone of the Alston Block and Northumberland Trough has an average thickness of about 50 feet and is the thickest of the Yoredale limestones. In general it is divisible into three parts (text-fig. 1): a lower dark-coloured limestone 2 or 3 feet thick, a central division of light-coloured limestone 25 to 30 feet thick, called the Main Posts, and an upper division of dark-coloured limestone with intercalated shales called the Tumbler Beds.

The lower division of the Great Limestone rests on either sandstone, shale, or a thin coal seam and there is often evidence of disconformity. The limestone is here even-bedded dark coloured and relatively unfossiliferous with few colonial corals and brachiopods. In micro-section the basal beds contain scattered angular quartz grains and argillaceous material with fairly abundant foraminifera and bryozoans. The argillaceous lower division of the Great Limestone is not of best quality for lime burning and is frequently left in place to form a hard quarry floor.

At the base of the central division of the Great Limestone lies the *Chaetetes* Band coralline biostrome. The band may be up to 3 feet thick and composed almost exclusively of tabular masses of *Chaetetes depressus* (Fleming); the limestone in the vicinity of the band is often dolomitic. Above the *Chaetetes* Band the Main Posts division of the limestone consists of thick beds of light-coloured limestone having conspicuous undulating or wavy bedding. In micro-sections the Main Posts are seen to be composed of fine shell and crinoid debris with abundant foraminifera and calcareous algae and quantities of fine-grained calcitic matrix. Calcareous algae are particularly numerous in the central and upper part of the division where the micro-fossil *Calcifolium bruntonense* sp. nov. is abundant and forms the Brunton Band. Near the top of the Main Posts division of the Great Limestone of the Alston Block and above the Brunton Band lies the Frosterley Band coralline biostrome. This band is persistent over the Alston Block and some neighbouring areas and is characterized by abundant simple corals particularly *Dibunophyllum bipartitum* (M'Coy). It is usually composed of several coralline beds divided by beds normal limestone and thin marl partings.

The upper division of the Great Limestone, called the Tumbler Beds, is composed of bands of even-bedded fragmental limestone separated by partings and bands of dark calcareous shale. The proportion of shale to limestone is very variable in the Tumbler Beds and locally the shales may be absent. Further information on this and other characters of the Great Limestone of the northern Pennines is given in Dunham (1948).

THE *CHAETETES* BAND

At Brunton Bank Quarry, Chollerford, near Hexham, Northumberland (grid ref. 35/928570), the *Chaetetes* Band is in the form of a bed varying between 1 and 3 feet in thickness. It is almost completely composed of compound corals surrounded and cemented by small quantities of yellow weathering dolomitic matrix. The band lies 3 feet above the base of the limestone and is overlain by a richly fossiliferous dark shale parting (text-fig. 1). Elsewhere the thickness and form of the *Chaetetes* Band varies considerably though the coral *Chaetetes depressus* is almost everywhere present as is the dolomitic matrix. In some places where *Chaetetes* has not been found the presence of other compound corals, particularly *Lonsdaleia laticlavia* S. Smith, in a dolomitic matrix is diagnostic of the *Chaetetes* Band horizon. In upper Allendale, Northumberland, where the development of *Chaetetes* is patchy and areas devoid of coral colonies occur, the dolomitic matrix is persistent. Similarly in the Barnard Castle neighbourhood, south Durham, a dolomitic band occurs 3 feet above the base of the Great (= Main) Limestone in which *Chaetetes depressus* has been found; the coral is not abundant and the *Chaetetes* Band is poorly developed in this area.

The form of the *Chaetetes* Band varies considerably from place to place due to variations in the amount of coralline material and matrix. At Brunton Bank the band is almost completely composed of tabular coral colonies piled one on top of the other; a similar development can be seen in a cutting by the Alston to Penrith road, 3 miles from Alston, Cumberland. The *Chaetetes* Band in these areas is in the form of large lenses which can be seen to thin out laterally to a narrow band in some places. At Killhope, upper Weardale, *Chaetetes* is not so abundant in the *Chaetetes* Band and occurs as isolated colonies up to 1 foot in diameter on a single bedding-plane. The colonies are evenly scattered on the bedding-plane which is 2 feet above the base of the Great Limestone and occur with colonies of *Lonsdaleia laticlavia* and *Syringopora*. Occasionally, as in the upper Eden valley south of Kirkby Stephen, Westmorland, the coralline material of the *Chaetetes* Band is separated by bands of limestone and may reach a total thickness of 5 feet or more.

Fauna. The fauna of the *Chaetetes* Band has been examined at Brunton Bank where it is particularly well exposed. The band is here almost completely composed of compound corals among which *C. depressus* is overwhelmingly predominant. Simple rugose corals and brachiopods occur in the dolomitic matrix between the tabular *Chaetetes* colonies but are not abundant. Where the underside of the *Chaetetes* colonies is visible a fauna of adherent bryozoans, annelids, brachiopods, &c., is found. The brachiopods are particularly interesting and include a new genus and species of leptaenoid form the affinities of which have yet to be fully deciphered. The following species have been recorded from the *Chaetetes* Band at Brunton Bank, Chollerford, Northumberland:

Aulopora ?, *Caninia cornucopiae* Michelin, *Chaetetes depressus* (Fleming), *Chaetetes septosus* (Fleming), *Cladochonus brevicollis* (M'Coy), *Dibunophyllum bipartitum* (M'Coy), *Diphyphyllum lateseptatum* (M'Coy), *Koninckophyllum echinatum* (Thomson), *Lithostrotion pauciradiale* M'Coy, *Lonsdaleia laticlavia* S. Smith, *Syringopora geniculata* (Phillips).

Serpula sp., *Spirorbis* cf. *laxus* Hall.

Archaeocidaris urei (Fleming), crinoid columnals up to 12 mm. diameter.

Fenestella spp., *Polypora sp.*, *Stenopora sp.*, indet. stick bryozoans.

Actinoconchus planosulcatus (Phillips), *Athyris lamellosa* (Léveillé), *Brachythyris decora* (Phillips), *Crania quadrata* (M'Coy), *Dictyoclostus pugilis* (Phillips), *Echinoconchus punctatus* (Martin), *Eomarginifera longispina* (J. Sowerby), *Overtonia fimbriata* (J. de C. Sowerby), *Rhipidomella michelini* (Léveillé), *Schellwienella crenistria* (Phillips), *Sinuatella sinuata* (de Koninck), *Spirifer sp.*, *Tylothyris* cf. *subconica castletonensis* North.

Known distribution. The *Chaetetes* Band is well developed in western Northumberland where it was first recognized and is known northwards in the Alnwick district. In south-west Northumberland it occurs in the Allendale area and is well developed near Allenheads and underground in Swinhope Mine. It is present in Weardale and Teesdale on the Alston Block, and occurs on the Pennine escarpment (Cumberland and Westmorland Pennines) and underground here in Silverband Mine (Dunham 1948, gives full details of the northern Pennine mines). On the west of the Pennine escarpment it has been found at King's Meaburn, near Appleby, in the Great Strickland (= Great) Limestone and farther south the *Chaetetes* Band is well developed in the upper Eden Valley near Kirkby Stephen, Westmorland. At the north-east corner of the Askrigg Block the *Chaetetes* Band has been recorded by Wells (1958) in the Richmond area, and farther south it may be present in Wensleydale where Hudson (1924) recorded a coral band at this position, but the exact fauna was not given.

THE BRUNTON BAND

This band lies towards the centre and top of the Main Posts division of the Great Limestone and is a persistent algal biostrome characterized by abundant remains of *Calcifolium bruntonense* sp. nov.—an algal genus new to this country. Algal limestones have previously been recorded from this position in Yoredale limestones (Hudson 1924) but *Calcifolium* is almost restricted to the Great Limestone where it is a conspicuous member of the algal limestone fauna.

At Brunton Bank Quarry the Brunton Band lies about 18 feet above the base of the Great Limestone and is of the order of 12 feet thick. It is formed of light grey-coloured limestone with occasional shaly partings and well-developed wavy-bedding, i.e. hummocky bedding-planes. The limestone is rather unfossiliferous except for the microfauna which is both varied and abundant; occasional brachiopods occur in the limestone. In micro-sections foraminifera and calcareous algae are conspicuous and invariably present with amounts of fine calcitic matrix. In Middle Tongue Beck, Great Dun Fell, Westmorland, the Brunton Band lies about 16 feet above the base of the Great Limestone and is some 19 feet thick; it lies directly below the Frosterley Band in this section. The position of the Brunton Band below the Frosterley Band appears to be general though occasional fragments of *Calcifolium*, perhaps derived fragments, have been found above the Frosterley Band.

The Main Posts division of the Great Limestone is very distinctive in the field but here the Brunton Band cannot be distinguished. In micro-sections, however, the presence of abundant *C. bruntonense* is easily recognizable (Pls. 30 and 31) and is diagnostic of the band. It is noteworthy that *C. bruntonense* is, as far as is known, almost restricted to the Main Posts of the Great Limestone. It has been found once in the underlying Four Fathom Limestone and once in the Five Yard Limestone at localities in western Northumberland. The abundance of *C. bruntonense* varies considerably through the thickness of the Brunton Band and also laterally from place to place. In general the organism is abundant in the central and upper parts of the band and sections from here may show the limestone to be packed with its remains.

Fauna and flora. The following species were recorded in micro-sections from the Brunton Band, Brunton Bank Quarry, Chollerford, Northumberland:

Calcifolium bruntonense sp. nov., Dasycladacian algae, *Girvanella sp. nov.* (tubules in contact laterally to form thin sheets).

Ammodiscids, Endothyrids, Nodosariids, Tetrataxiids, Textulariids.

Fragmental organic debris including: small rugose corals indet., *Archaeocidaris sp.* [radioles and plates], small crinoid columnals, indet. bryozoans, brachiopod and gastropod shells, ostracods.

Known distribution. The Brunton Band is well developed in western Northumberland, where the organism was first discovered, and has been traced as far northwards as the Morpeth district, central Northumberland. On the Alston Block it occurs below the Frosterley Band and is well developed in the Westmorland and Cumberland Pennines. The Brunton Band is present in the Barnard Castle area of south Durham and has been recorded by Dr. H. Ll. L. Jones in the Middleton in Teesdale district. Farther south on the eastern side of the Askrigg Block it has been found by Dr. A. J. Wells in the area north of Richmond and by Dr. A. A. Wilson in Coverdale, south-west of Leyburn, Yorkshire.

THE FROSTERLEY BAND

This is a persistent though lenticular coralline biostrome characterized by abundant remains of simple rugose corals particularly *Dibunophyllum bipartitum* (M'Coy). It lies normally about 24 feet below the top of the Great Limestone and varies between a foot and 3 feet in thickness except where it is divided by beds of limestone when it may be considerably thicker. At Harehope Quarry (grid ref. 45/037365), south-east of Frosterley in Weardale, where for many years stone from the band has been wrought for ornamental purposes under the name Frosterley Marble, the band is divided by beds of limestone into several coralline horizons the general section of which is as follows:

Grey crinoidal limestone		
Frosterley Band	Coralline limestone with *Dibunophyllum*	6″
	Grey fragmental limestone	9″
	Coralline limestone with *Dibunophyllum*	3″
	Grey limestone with compound corals	2′ 0″
	Coralline limestone with *Dibunophyllum*	1′ 6″
	Grey fragmental limestone	6″
	Coralline limestone with *Dibunophyllum*	4″
	Grey fragmental limestone	2′ 0″
	Coralline limestone with *Dibunophyllum*	3″
	Grey fragmental limestone	1′ 3″
	Coralline limestone with *Dibunophyllum*	1′ 6″
Grey fragmental limestone		

A similar section occurs at Greenfield Quarry, one mile north-north-west of Cowshill in Weardale (grid ref. 35/852423). In other areas such as the Great Dun Fell district, Westmorland Pennines, the Frosterley Band occurs as a single stratum within the limestone. The discontinuous nature of the Frosterley Band is not a conspicuous feature and the individual lenses must be of considerable extent. The lenticular nature of the band is well seen in Greenfield Quarry, Cowshill, where a richly fossiliferous coralline bed 2 feet thick can at one point be seen to die out within 2 yards along the quarry face.

The fauna of the Frosterley Band is very distinctive, being composed of abundant simple rugose corals, mainly *Dibunophyllum*, *Koninckophyllum*, *Aulophyllum*, and *Caninia*, with some brachiopods and few compound rugose corals, usually *Lonsdaleia* and *Diphyphyllum*. The simple corals are frequently found in a rolled condition and partly devoid of epitheca, very few are found in position of growth, most lie almost horizontally in the limestone matrix and some are overturned. Some of the colonies of *Lonsdaleia* also occur overturned in the Frosterley Band and provide further evidence of strong current action during or shortly after deposition. It seems possible that the discontinuous nature of the Frosterley Band may in part be due to current scouring.

Fauna. Although compound rugose corals and brachiopods occur in the Frosterley Band they are everywhere relatively insignificant compared with an overwhelming predominance of simple corals particularly *Dibunophyllum bipartitum* (M‘Coy); this species is of particular interest in the band owing to the high degree of variation which it shows (Johnson 1956). At Harehope Quarry, near Frosterley in Weardale, the Frosterley Band fauna includes the following species:

Aulophyllum fungites (Fleming), *Caninia cornucopiae* Michelin, *Dibunophyllum bipartitum* (M‘Coy), *Diphyphyllum lateseptatum* (M‘Coy), *Koninckophyllum echinatum?* (Thomson), *K. interruptum* Thomson and Nicholson, *Lonsdaleia laticlavia* S. Smith.

Brachythyris sp., *Dielasma sp.*, *Dictyoclostus pugilis* (Phillips), *Gigantoproductus latissimus* (J. Sowerby) group, *Pugnax pugnus* (Martin), *Spirifer sp.*

Known distribution. The Frosterley Band appears to be more restricted in distribution than the other faunal bands in the Great Limestone and is only well developed on the Alston Block. Northwards it does not appear to extend far beyond the Stubblick fault line, the northern boundary of the block, though scattered simple corals do occur at about the correct horizon in some areas to the north, e.g. the Chollerford area, Northumberland. The band is particularly well developed in Weardale and Teesdale and is present on the Pennine escarpment. To the south of the Alston Block it has been recorded by Reading (1957) in the Cotherstone Syncline, and Wells (1958) at the north-east corner of the Askrigg Block, while Mr. Selwyn Turner has shown the writer a probable thin representative of the band in the upper Eden Valley south of Kirkby Stephen, Westmorland.

SYSTEMATIC PALAEONTOLOGY

GREEN ALGAE

Class CHLOROPHYCEAE

Order SIPHONALES

Family CODIACEAE

Genus CALCIFOLIUM Shvetzov and Birina 1935

Type species *Calcifolium okense* Shvetzov and Birina

In 1935 Shvetzov and Birina described *C. okense* from limestones of the Upper Okian Series, Upper Viséan (Lower Carboniferous), of the Moscow Basin but they did not give an exact generic diagnosis. Maslov (1956, p. 48) gives a generic diagnosis as follows:

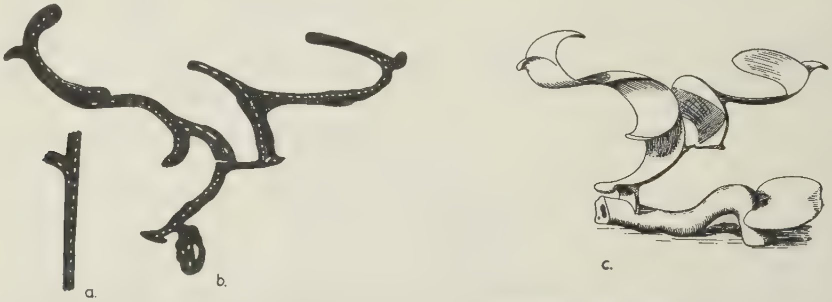
> Thallus is composed of a cylindrical pipe-like siphon at first rather large and then branching dichotomously into pipes of constant diameter. Around the pipes a calcareous crust is deposited resulting in a calcareous skeleton of the following form. Attached to a cylindrical hollow-bodied calcareous stem are thin plates pierced by dichotomously branching canals which either fill the whole of the calcareous plate or are found only on one side of it. The plates branch to form other plates and are usually slightly curved. Organs of multiplication have not been observed.

Remarks. Maslov (1956) restricted *Calcifolium okense* Shvetzov and Birina, retaining in *C. okense* only those forms with a single series of canals in the upper surface of the plates, and placing forms with two or three series of canals in a new species *C. punctatum* Maslov. In his description of *C. okense*, Maslov details the exact form of the thallus and on his pl. 10, fig. 5 and text-fig. 7*b* he figures the specimen of a complex branched plate which allowed the reconstruction of the whole of the skeleton; the text-figure (Maslov 1956, text-fig. 7*b*) is reproduced here (text-fig. 2*b*). Shvetzov and Birina (1935) did not commit themselves on the reconstruction of *Calcifolium* more than to suggest that the organism they describe must represent flat, broad leaves or blades having a network of canals nearer to one surface. Maslov (1956) devotes several paragraphs to the form and reconstruction of *Calcifolium* and shows that the organism is composed essentially of a hollow tubular central stem from which arise complex platy branches. The most probable reconstruction of *Calcifolium* according to Maslov is given on text-fig. 9*b* of his 1956 paper which is reproduced here (text-fig. 2*c*).

Calcifolium bruntonense sp. nov.

Plates 30 and 31; text-fig. 3*a*-*b*

Diagnosis. *Calcifolium* with large hollow branching tubular stem (siphon), initially 1 mm. in diameter, from which numerous complex smooth platy branches arise. Stem wall between 100 and 200 μ thick and containing a series of irregular tubular canals which connect with canals in the lateral branches. Lateral branches are expanded distally, between 100 and 150 μ thick, and form wide plates which surround the central stem at the position of attachment. They contain a well-developed series of subcentrally placed dichotomously branching parallel canals. The branches fork to form complex fronds of large and small curved branches.



TEXT-FIG. 2. Transverse sections and reconstruction of *Calcifolium* (after Maslov 1956). (*a*) Transverse section of a forking branch of *C. okense*, ×50 (Maslov 1956, text-fig. 7*a*). (*b*) Drawing of a complex branched frond of *C. okense* which allowed the reconstruction of the whole skeleton, missing parts have been restored, ×50 (Maslov 1956, text-fig. 7*b*). (*c*) The most probable reconstruction of *Calcifolium* according to Maslov (1956, text-fig. 9*b*).

Holotype. The specimen figured in Pl. 31, fig. 6; Brunton Band, Great Limestone, Brunton Bank Quarry, Chollerford, Northumberland (35/928570); basal Namurian, E_1 Zone (basal Upper Carboniferous). Geological Survey and Museum, London, reg. no. PF 619.

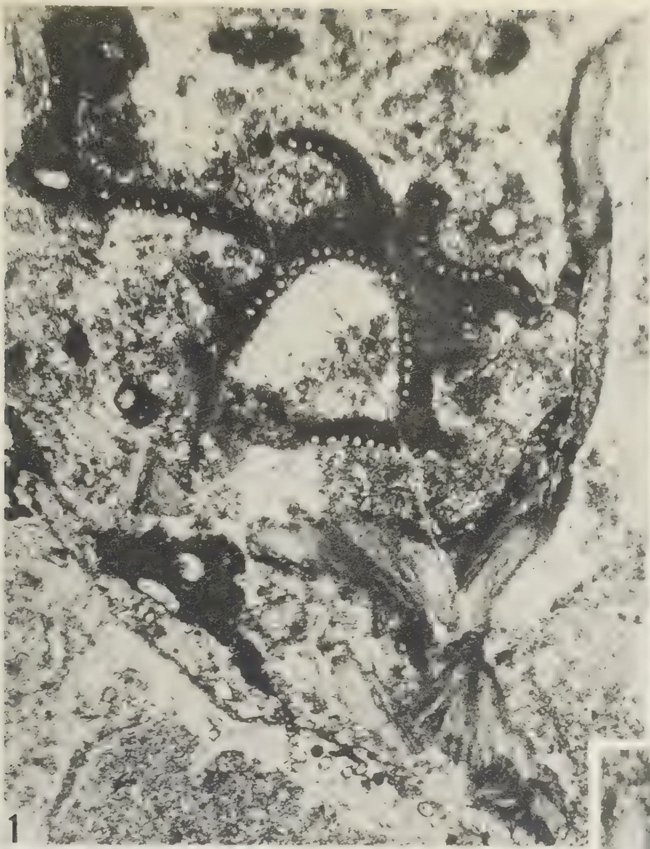
Paratypes. The specimens figured in Pl. 30, figs. 1–4 and Pl. 31, figs. 1–5, 7; same geological horizon as the holotype. Geological Survey and Museum, London, reg. nos. PF 617–618 and PF 620–622. Slides PF 617–618 from quarry 750 yards west 20° north of Grindon Hill House, Haydon Bridge, Northumberland (35/823684); slide PF 620 from Brunton Bank Quarry, Chollerford, Northumberland (35/928570); slide PF 621 from quarry 300 yards north-east of Beamwham Farm, Haydon Bridge, Northumberland (35/814684); slide PF 622 from quarry 100 yards east of Common House, Haltwhistle, Northumberland (35/718660).

Horizon. Abundant towards the centre and top of the Main Posts division of the Great Limestone, basal Namurian, E_1 Zone, Upper Limestone Group, Carboniferous Limestone Series of northern England. Locally it occurs in the underlying Four Fathom Limestone, uppermost Viséan, P_2 Zone, Middle Limestone Group, Carboniferous Limestone Series.

EXPLANATION OF PLATE 30

Figs. 1–4. *Calcifolium bruntonense* sp. nov., paratypes, approximately ×40. 1, Lateral branch in transverse section showing forking (top centre), fragment of lateral branch (right), wall of central stem showing internal canals (bottom left), PF 617. 2, Transverse and tangential section of a forking branch, PF 620. 3, Transverse and tangential sections of branches, PF 621. 4, Series of branches in longitudinal section showing forking at the distal extremity, PF 617.

Brunton Band, Great Limestone. PF 617 from Grindon Hill, Haydon Bridge; PF 620 from Brunton Bank Quarry, Chollerford; PF 621 from Beamwham Farm, Haydon Bridge.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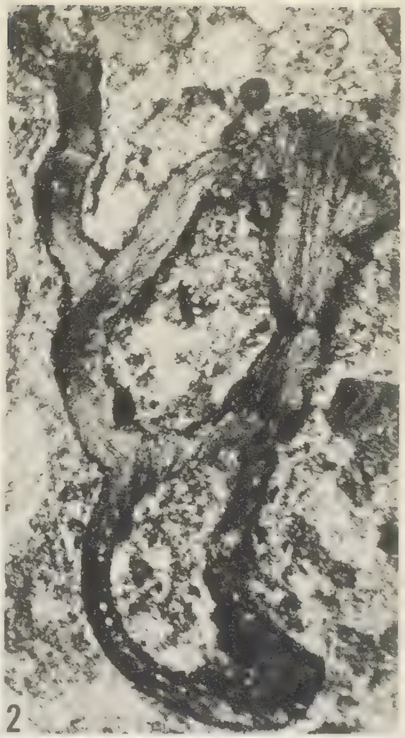
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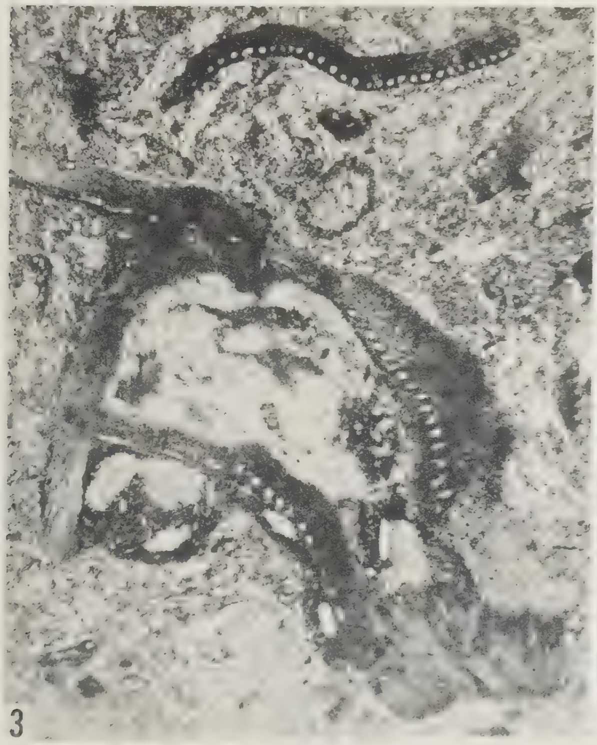
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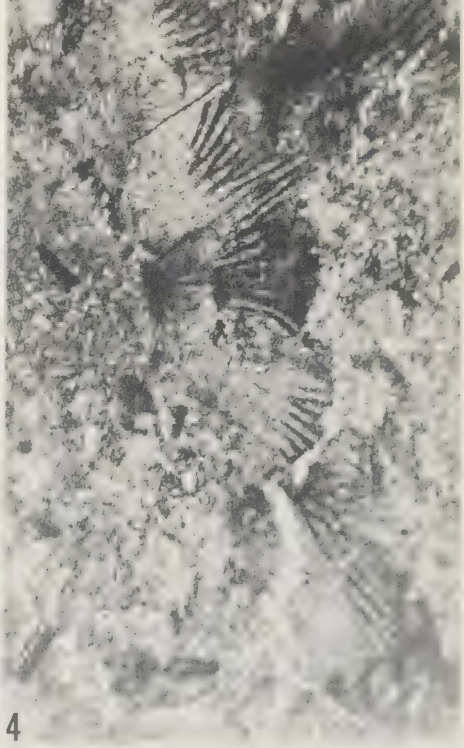
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JOHNSON, *Calcifolium bruntonense* sp. nov.

Dimensions. The following table shows the comparative dimensions of *C. bruntonense* sp. nov. and *C. okense* Shvetzov and Birina em. Maslov taken from Maslov (1956, p. 48):

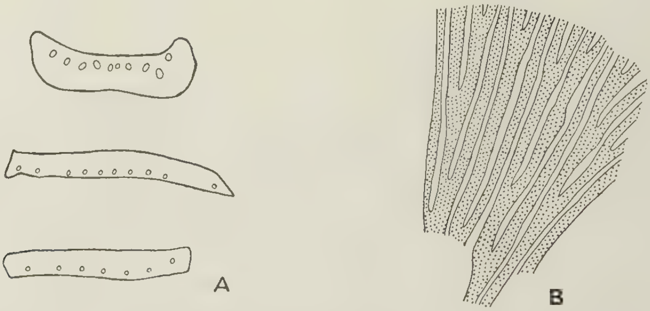
	C. bruntonense	*C. okense*
Diameter of central stem	1 mm.	0·3 to 0·4 mm.
Thickness of walls of the central stem . .	100–200 μ	70–100 μ
Diameter of central stem wall canals . .	40 μ	. .
Length of individual branches, maximum. .	2 mm.	. .
Thickness of lateral branches	100–150 μ	70–100 μ
Diameter of canals in branches . . .	20–50 μ	16 μ
Angle of forking in canals	15°	10–25°
Distance between canals	15–20 μ	0–40 μ

Description. C. bruntonense is only visible in micro-sections of limestone and is normally seen as small narrow parallel-sided curved strips averaging 100–150 μ across (Pl. 31, figs. 5–7; text-fig. 3*a*). These fragments are transverse sections of broken lateral branches and show the internal system of canals as a row of small circular pores nearer to one margin. Sections of complete branches and the central stem are more rare. The central stem (Pl. 30, fig. 1; Pl. 31, fig. 1) is an irregularly curved hollow tube with walls up to 200 μ thick which contain a series of canals about 40 μ in diameter. These canals are irregularly spaced in the stem wall and appear to take a sinuous path. The central stem is initially 1 mm. thick but becomes narrower towards the distal extremity. The hollow central cavity of the stem may be divided by extensions of the wall into separate chambers but the evidence for this is at present inconclusive. The lateral branches are given off from the sides of the central stem (Pl. 30, fig. 1; Pl. 31, figs. 1, 6) and appear to surround it at the position of attachment. The branches are narrow near the base and expanded distally, usually curved and with slightly rounded margins. They are quite smooth and devoid of ornament and are almost uniform in thickness throughout. The primary branches given off from the central stem fork repeatedly to form complex fronds (Pl. 30, figs. 1–4; Pl. 31, figs. 2, 6). Forking seems to take place near the distal margin of the branches and is irregular. Within the lateral branches the canal system shows up conspicuously in both longitudinal and transverse sections. In longitudinal sections the canals are seen to be parallel and closely spaced at rather less than a canal width apart (Pl. 30, fig. 2; text-fig. 3*b*). The canals are of almost constant width, between 20 and 50 μ diameter, in individual branches but increase in number steadily by repeated forking. At the proximal extremity the canal system commences with a small number of canals which appear to unite at the base (Pl. 31, figs. 3, 4). The branching of the canals is dichotomous in each case and is frequently repeated again on both forks so formed though not necessarily at the same distance from the initial branching (text-fig. 3*b*). The canals increase in diameter near the position of branching and occasionally show slight swelling without branching taking place. The exact form of termination of the canals at the distal extremity is not known, though the canals are thought to lie nearer to the surface of the branch in this region.

Remarks. There is a striking similarity between specimens of *C. bruntonense* sp. nov. and *C. okense* Shvetzov and Birina em. Maslov which is immediately evident from Maslov's figures. In particular Maslov's text-figure (1956, text-fig. 7*b*) of a complex branch of

C. okense, herein reproduced in text-fig. 2*b*, is generally similar to the *C. bruntonense* frond in Pl. 30, fig. 1 (top centre). Also the specimen of *C. okense* figured by Shvetzov and others (1937, pl. 1, fig. 3) is readily comparable with the fragment of *C. bruntonense* shown in Pl. 30, fig. 1 (right-hand side). There seems little doubt but that the species are reliably congeneric.

C. bruntonense differs from *C. okense* in its larger size, different arrangement of the canals in the lateral branches, and apparent differences in the shape of the branches and their arrangement on the central stem. Both central stem and fronds are larger in *C. bruntonense*, the lateral branches are thicker and their internal canals have a larger diameter. The branches also tend to expand outwards and are not oval as in *C. okense*, they appear to be more closely spaced on the central stem and are generally less branched (Pl. 30, fig. 4). Within the lateral branches the canals are parallel, i.e. less divergent than in *C. okense* and the individual canals are more closely spaced and regular. The dichotomous branching of the canals tends to be more frequent, and the angle of divergence of the canals at the position of branching differs in being constant at 15°. *C. bruntonense* differs from *C. punctatum* in the presence of only a single series of canals within the lateral branches.



TEXT-FIG. 3. *Calcifolium bruntonense* sp. nov. (A) Transverse and tangential sections of branch fragments, ×30, PF 621; (B) detail of dichotomously branching canals in a lateral branch, longitudinal section ×50, PF 622.

The geological horizon of the Russian material is of interest. *C. okense* and *C. punctatum* have been recorded from the Upper Okian marine limestones, the Alexin, Mikhailov, and Venev beds, of the Moscow Basin and from the Urals. According to Shvetzov and others (1937, p. 14) the genus is characteristic of the Okian Series and are particularly

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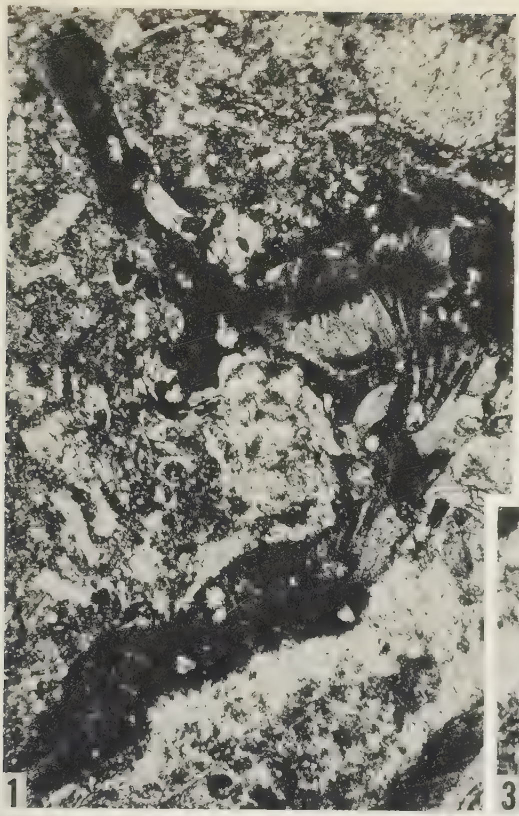
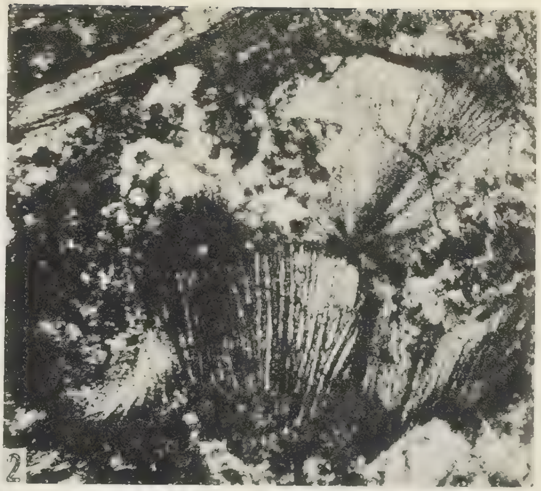
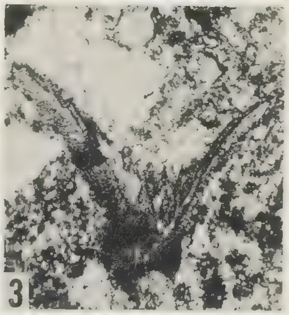
EXPLANATION OF PLATE 31

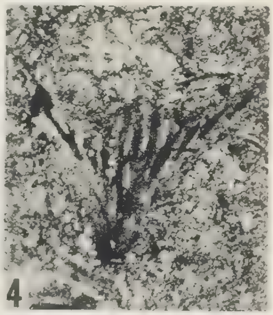
Figs. 1–7. *Calcifolium bruntonense* sp. nov., holotype and paratypes, approximately ×40. 1, Section of wall of the central stem showing point of attachment of a lateral branch, PF 621. 2, Lateral branches in longitudinal section showing forking, PF 622. 3, Base of a lateral branch, PF 618. 4, Base of a lateral branch showing canals, PF 617. 5, Transverse section of a branch, PF 620. 6, Holotype, transverse and tangential sections of branches with central stem in cross-section, PF 619. 7, Transverse section of a branch showing forking, PF 617.

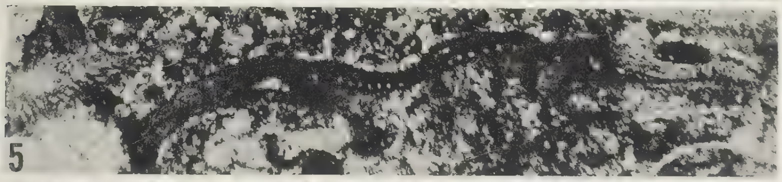
Brunton Band, Great Limestone. PF 617–618 from Grindon Hill, Haydon Bridge; PF 619–620 from Brunton Bank Quarry, Chollerford; PF 621 from Beamwham Farm, Haydon Bridge; PF 622 from Common House, Haltwhistle.

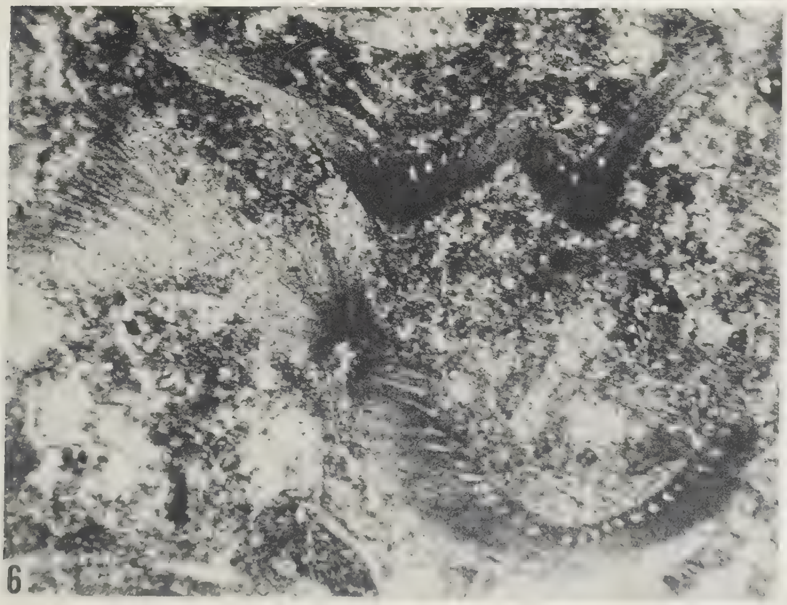


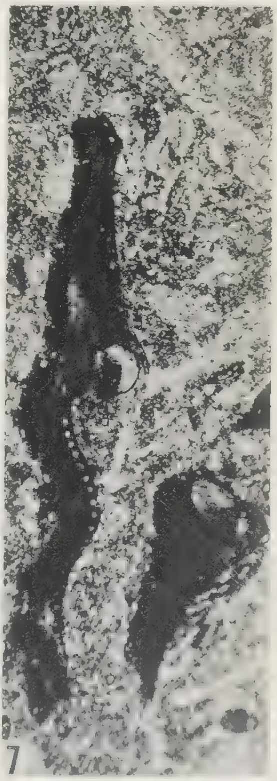












JOHNSON, *Calcifolium bruntonense* sp. nov.

abundant in the Mikhailov and Venev beds at the top. The presence of *Goniatites granosus* Portlock in the Mikhailov Beds (ibid., p. 13, footnote) indicates a P_2 age Viséan. And the Tarussa Beds, at the base of the Serpukhovian Series which overlies the Okian, has yielded *Cravenoceras* (ibid., p. 16; see also Ramsbottom 1957, p. 305) indicative of the E Zone, Namurian. The Viséan–Namurian junction must therefore lie in the vicinity of the top of the Okian Series and thus *Calcifolium* occurs at a similar horizon in the Carboniferous successions of the Moscow Basin and northern England.

Note. C. bruntonense was originally found by the writer in 1949 and has since then been known to other workers in the northern Pennines under the name *Organism* 'α' Johnson.

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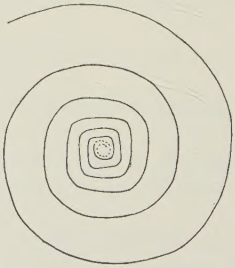
NOTE

ENTOGONITES CF. *BOREALIS*, AN ALASKAN GONIATITE FROM IRELAND

by FRANK HODSON

AT Cashel in County Fermanagh near the border of the Six Counties and about two miles from Kiltyclogher, Co. Leitrim, is a disused Carboniferous Limestone quarry, at the base of which occurs a fossiliferous shale. The main elements of the fauna, as collected by Mr. E. W. J. Moore and the writer, are corals, amongst which *Caninia*, *Rylstonia*, *Cyathaxonia*, and other simple corals are very numerous. Tabulate corals, brachiopods, and rare trilobites are also found, together with an interesting goniatite assemblage which dates the shale as belonging to the upper part of the B_2 Zone of the English goniatite zonal scheme, and about the level of faunal band Co 1 of Cowdale Clough, Barnoldswick, Yorkshire (Bisat 1952, p. 158). The present note records the occurrence of a species of the rare goniatite genus *Entogonites* Kittl 1904 (type species *Tetragonites grimmeri* Kittl) which seems, so far as the state of preservation permits it to be named, to be near the newly described species *E. borealis* Gordon. The type material of this species occurs in Alaska (Gordon 1957, p. 53).



TEXT-FIG. 1. Nearly median section in plane of coiling of *Entogonites* cf. *borealis* Gordon from Cashel, Co. Fermanagh, Northern Ireland; × 4.

Entogonites differs markedly from *Nomismoceras* (which is a common element of the Cashel goniatite fauna) in the quadrangular coiling of the inner whorls. The single specimen of *Entogonites*, here reported, is indifferently preserved and one side was particularly poor. A nearly median section in the plane of coiling was therefore prepared from the poorly preserved side, which revealed the coiling characteristic of the inner whorls (text-fig. 1). This plainly showed the quadrangular early coiling characteristic of *Entogonites*. Similar sections prepared from specimens of *Nomismoceras* from the same bed showed the normal logarithmically coiled spiral.

E. borealis Gordon differs from *E. grimmeri* (Kittl) in possessing fewer, blunter ribs. Thus *E. grimmeri* has 45–50 sharp ribs, while the adult *E. borealis* has 35–40 blunter ribs. The Irish specimen has about 30, but this count also occurs on younger whorls of *E. borealis*. In such characters as are sufficiently preserved to permit accurate comparison, the Irish specimen compares well with *E. borealis*, but because of its poor preservation it is probably best referred to as *E.* cf. *borealis*, and makes an interesting link with the newly described Arctic American goniatite fauna.

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